RESEARCHES ON FUNGI

VOL. II.

A. H. REGINALD BULLER

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RESEARCHES ON FUNGI

VOLUME II

BY THE SAME AUTHOR

RESEARCHES ON FUNGI

VOLUME I. An Account of the Production, Liberation, and Dispersion of the Spores of Hymenomycetes treated Botanically and Physically. Also some Observations upon the Discharge and Dispersion of the Spores of Ascomycetes and of Pilobolus. With 5 Plates and 83 Figures in the Text. Royal 8vo, 12*s*. 6*d*. net.

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RESEARCHES ON FUNGI

VOLUME II

FURTHER INVESTIGATIONS UPON THE PRODUCTION AND LIBERATION OF SPORES IN HYMENOMYCETES

BY

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WITH ONE HUNDRED AND FIFTY-SEVEN FIGURES IN THE TEXT

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TO

GULIELMA LISTER

WHOSE BRILLIANT REVISION OF HER FATHER'S
MONOGRAPH OF THE MYCETOZOA HAS
ENRICHED BOTANICAL LITERATURE

PREFACE

In 1909 there was published my *Researches on Fungi*, which treated of the fruit-bodies of Hymenomycetes and certain Ascomycetes considered as organs for the production and liberation of spores. During the thirteen years which have elapsed since that time my investigations have been continued, and I now propose to embody the results which have accumulated therefrom in three new volumes. The 1909 volume and these new volumes are to be considered as parts of a larger work having the general title *Researches on Fungi*. Of this work the 1909 volume now becomes Volume I and the present volume Volume II. The third and fourth volumes are already in an advanced stage of preparation for the press.

The morphological and physiological facts which have come to light in the course of my researches have taught me that the adaptation of structure to function in the higher fungi is just as remarkable as that found in the Phanerogamia. The form and arrangement of parts exhibited in the sporophore of the Common Mushroom and its allies appear to be no less beautifully fitted for the efficient production and liberation of spores than are the form and arrangement of Orchid flowers for securing successful pollination by insects. Ample evidence supporting this conclusion will, I believe, be found in the pages of this book. The analysis of the hymenium of *Panaeolus campanulatus*, as described in Chapter X, will perhaps enable the reader to comprehend, in a manner not hitherto possible, how millions of hyphae combine their activities to produce the spore-stream which is emitted from beneath the pileus without a moment's interruption for the seven or more days of the spore-fall period.

The work for this volume has been carried out chiefly in my own laboratory at the University of Manitoba, but in part also in the

Herbarium of the Royal Botanic Gardens at Kew and in the Botanical Department of the University of Birmingham. It is with much pleasure that I here acknowledge the courtesy of the authorities at Kew and Birmingham for the facilities accorded me.

Of the one hundred and fifty-seven illustrations, all but twelve are here published for the first time. The source of each borrowed illustration is duly acknowledged in the text. Of the seventy-seven drawings, sixty-nine were executed by my own hand. Of the eighty photographs, thirty-one were made under my direction; and the others, with the exception of four taken from previous publications, were very kindly contributed by friends and correspondents: fourteen by A. E. Peck; eleven by Somerville Hastings: three each by J. E. Titley, J. H. Faull, and C. J. Humphrey; two each by Miss E. M. Wakefield, C. W. Lowe, B. Leeper, and W. S. Odell; and one each by G. G. Hedgcock, R. Hancock, and W. B. Grove, the last having been taken by the late J. Edmonds.

I desire to thank my numerous correspondents in both Europe and North America for assisting me by sending specimens of fungi and reprints of papers, and by supplying information of various kinds in response to my enquiries. Dr. Guy Barlow has been good enough to help me with the sections relating to the revised formula for Stokes' Law. In the final revision of the proofs, my friend, W. B. Grove, M.A., has again given me the benefit of his wide mycological knowledge and experience.

Finally, I wish to express my indebtedness to the Birmingham Natural History and Philosophical Society for a grant of £25 toward the cost of making the blocks for the illustrations of this volume, and to the Canadian National Council for Scientific and Industrial Research for a grant of $1,000 toward the expense of producing this volume and the two which are to follow it.

A. H. REGINALD BULLER.

WINNIPEG, *October* 22, 1922.

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The Elements of the Hymenium. — The investigations of numerous observers have led to the conclusion that the hymenium of Hymenomycetes, when most fully developed, consists of three kinds of elements : basidia, paraphyses, and cystidia.

The essential element of the hymenium, always present under normal conditions, is the basidium. Typically, this is a club-shaped cell which, on attaining maturity, projects slightly from the general surface of the hymenium and bears at its free end four sterigmata and four spores. While the vast majority of species have basidia of this type, there are exceptions to the general rule. Thus monosporous basidia are characteristic of *Pistillaria maculaecola*, disporous of the cultivated Mushroom (*Psalliota campestris*), trisporous of *Coprinus narcoticus*, hexasporous of *Cantharellus cibarius*, and octosporous of *Corticium coronatum*. These and other aberrant types of basidia will be treated of more fully in Chapter X in a discussion of the relative position of the sterigmata.

Paraphyses are elements which more or less resemble the bodies

of basidia, but do not bear sterigmata and spores. They are destined to remain sterile from the first. The early investigators of the hymenium, Léveillé,[1] Berkeley,[2] Corda,[3] and others, believed that the majority of the cells associated with the basidia remain sterile. In 1842, Montagne,[4] who held the same opinion, gave to these sterile cells the name of *paraphyses* and described them as "elongated, tubular, caeciform cells, placed parallel the one to the other, like the pile of velvet." Later on, certain observers expressed doubt whether true paraphyses exist. Thus, in 1862, Hoffmann[5] stated that in Coprinarius every hymenial cell becomes a fertile basidium. De Seynes, in 1864, admitted that, in general, paraphyses in the Hymenomycetes are sterile cells analogous to the paraphyses of the Discomycetes,[6] but in 1867 he expressed the view that in *Fistulina hepatica* the hymenium consists of basidia only.[7] Levine[8] more recently has said: "It seems to me that in all cases the paraphyses are really immature basidia." That paraphyses, except in the genus Coprinus, are simply basidia destined to become fertile, is a view also held by Ruhland[9] who described them as "nothing more than young basidia which have not yet attained full development," by Demelius[10] who has defined them as "derzeit nicht fertile Basidien," and by René Maire[11] who calls them "basides

[1] J. H. Léveillé, "Recherches sur l'Hyménium des Champignons," *Ann. Sci. Nat.*, 2 sér., T. VIII, 1837, pp. 321–338.

[2] M. J. Berkeley, "On the Fructification of the Pileate and Clavate Tribes of Hymenomycetous Fungi," *Ann. Nat. Hist.*, London, vol. i, 1838, pp. 81–101.

[3] A. C. I. Corda, *Icones Fungorum*, T. III, 1839, etc.

[4] C. Montagne, "Organographic and Physiologic Sketch of the class Fungi," Translated by Berkeley, *Ann. and Mag. of Nat. Hist.*, vol. ix, 1842, p. 288.

[5] H. Hoffmann, *Icones analyticae Fungorum*, Giessen, Heft II, 1862, p. 46.

[6] De Seynes, "Aperçus sur quelques points de l'organisation des champignons supérieurs," *Ann. Sci. Nat.*, 5 sér., T. I, 1864, pp. 243–244.

[7] De Seynes, "Recherches sur quelques points de l'anatomie du genre Fistulina," *Compt. rend.*, T. LXIV, 1867, pp. 426–429.

[8] M. Levine, "Studies in the Cytology of the Hymenomycetes, especially the Boleti," *Bull. Torrey Bot. Club*, vol. xl, 1913, p. 133.

[9] W. Ruhland, "Zur Kenntnis der intracellularen Karyogamie bei den Basidiomyceten," *Bot. Zeit.*, Jahrg. LIX, 1901, Abt. 1, pp. 199–200.

[10] Frau Demelius, "Beitrag zur Kenntnis der Cystiden," *Verh. der k. k. Zool.-Bot. Gesells. in Wien*, Bd. LX, 1911, p. 279.

[11] René Maire, "Recherches cytologiques et taxonomiques sur les Basidiomycètes," *Bull. Soc. Myc. France*, T. XVIII, 1902, p. 187.

jeunes." De Bary,[1] Fayod,[2] and others, however, have regarded paraphyses as distinct from basidia. My own observations made during the last thirteen years have convinced me that this view is the correct one. I shall presently describe new methods for distinguishing the hymenial elements from one another, and shall show that with their help it has been possible to determine that paraphyses, *i.e.* cells which in general resemble immature basidia but which are destined from the first to remain sterile, are present in the hymenium of various species of Coprinus, *Psathyrella disseminata*, *Panaeolus campanulatus*, *Anellaria separata*, *Stropharia semiglobata*, *Psalliota campestris*, *Galera tenera*, *Bolbitius flavidus*, and *Lepiota cepaestipes*.

During the gradual exhaustion of the hymenium by the production and liberation of spores, the paraphyses lose all their protoplasm except a very thin wall-layer and, at the same time, become greatly swollen. The manner in which they assist the basidia to perform their functions will be discussed subsequently in connection with the description of various hymenia.

Cystidia, like paraphyses, are sterile elements, but they differ from these in their larger size, their peculiar form, their smaller number, and frequently in the nature of their cell-walls and of their contents. They are present in some species and not in others. In some species where they occur, but not in all, they produce characteristic excretions, while in certain Coprini they have a mechanical function. They will be treated of more fully in Volume III.

It is now known that the two nuclei present in each basidium from the beginning of its differentiation fuse together and thus consummate a sexual act of which the first stages take place in the mycelium.[3] According to Ruhland,[4] the well-marked paraphyses of *Coprinus porcellanus* at first, like the basidia, contain two nuclei; but these two nuclei never fuse and, finally, as the paraphyses swell up and become poorer and poorer in protoplasm, undergo degeneration. Ruhland also found pairs of nuclei in the large

[1] A. de Bary, *Vergleichende Morph. u. Biol. der Pilze*, Leipzig, 1884, p. 326.

[2] V. Fayod, "Prodrome d'une Histoire Naturelle des Agaricinés," *Ann. Sci. Nat.*, T. IX, 1889, p. 253.

[3] *Vide infra*, vol. iv.

[4] W. Ruhland, *loc. cit.*

cystidia of *Coprinus atramentarius*; but, here again, no nuclear fusions could be observed. It thus appears that paraphyses and cystidia differ from basidia in their nuclear behaviour.

The Discharge of Spores from the Basidia.—The discharge of spores from their basidia was first observed in 1843 by Schmitz who studied the hymenium of the living fruit-bodies of *Thelephora sericea* (probably *Stereum hirsutum*). He discovered that the four spores of each basidium are discharged *in succession*.[1] Brefeld, in 1877, stated that the four spores of each basidium of *Coprinus stercorarius* are shot off simultaneously.[2] Zalewski, in 1883, gave an account of some observations on species of Coprinus and Russula, and upon *Cantharellus cibarius*, which afforded evidence that the spores of each basidium in these species are often shot off in succession.[3] Fayod, in 1889, stated that successive discharge takes place in *Galera tenera*.[4] Finally, in 1909, in the first volume of this work, I showed by means of detailed observations made upon a number of species of Hymenomycetes that successive discharge of the four spores of each basidium is the rule, and that simultaneous discharge is either very rare or never occurs at all.[5]

That the spores are *violently* projected from their basidia was first asserted by Brefeld[6] in the account of his investigations on *Coprinus stercorarius* and *Amanita muscaria*. Zalewski[7] and Fayod,[8] who used other species, confirmed Brefeld's observations. In 1909, by employing precise methods, I established the fact of violent projection for the Hymenomycetes in general.[9]

Brefeld,[10] in his foot-note on the discharge of spores in *Coprinus stercorarius*, asserted that after discharge drops of water are left on

[1] J. Schmitz, "Beiträge zur Anatomie und Physiologie der Schwämme," *Linnaea*, Bd. XVII, 1843, p. 434.

[2] O. Brefeld, *Botanische Untersuchungen über Schimmelpilze*, Heft III, 1877, pp. 65–66.

[3] A. Zalewski, "Über Sporenabschnürung und Sporenabfallen bei den Pilzen," *Flora*, Bd. LXVI, 1883, p. 266.

[4] V. Fayod, *loc. cit.*, p. 272.

[5] A. H. R. Buller, *Researches on Fungi*, vol. i, 1909, pp. 144–146.

[6] O. Brefeld, *loc. cit.*, pp. 65, 66, and 132.

[7] Zalewski, *loc. cit.*

[8] V. Fayod, *loc. cit.*, pp. 271–272.

[9] A. H. R. Buller, *loc. cit.*, vol. i, Chap. X, pp. 120–147.

[10] O. Brefeld, *loc. cit.*, pp. 65–66.

the tops of the sterigmata and that the spores carry part of the fluid contents of the burst basidium with them. Zalewski,[1] who worked with several species of Hymenomycetes, denied that drops are left on the sterigmata after discharge. Without knowing of Zalewski's observations, I, too, failed to find the drops. In the first volume of this work I said : " At the moment of discharge of the spores from the basidia of *Coprinus comatus*, *Polyporus squamosus*, etc., I have endeavoured to observe drops on the vacant sterigmata, but without success ; nor, by using my Method I, have I been able to detect drops on any spores as soon as they have settled on glass immediately after leaving the basidia." [2] Fayod, in his account of spore-projection, makes no mention of any drop left on a sterigma *after* spore-discharge or on a discharged spore, but he discovered that in *Galera tenera* a drop of water is formed at the hilum of the spore (*i.e.* near the place where the spore joins the sterigma) *before* discharge takes place.[3]

When the first volume of this work was published, I had not seen any drop arise at the base of a spore. However, in 1910, when studying some fruit-bodies of *Coprinus curtus* with the high power of the microscope, I rediscovered the phenomenon of drop-excretion just before spore-discharge. Afterwards I found that my observations simply confirmed those of Fayod which had been made twenty-two years previously.[4] Further and much more extensive studies of spore-discharge have convinced me that throughout the Hymenomycetes it is an invariable rule that, *just before a spore is to be violently projected, a water-drop is excreted at its base.* The results of my investigations will now be given in detail.

Calocera cornea has tiny orange-yellow finger-shaped fruit-bodies which are not infrequently seen on decaying stumps of trees in the

[1] Zalewski, *loc. cit.*, p. 266.

[2] A. H. R. Buller, *loc. cit.*, pp. 148–149.

[3] V. Fayod, *loc. cit.*

[4] Fayod's observations on *Galera tenera* are recorded in a single paragraph (*loc. cit.*, p. 272) and are not accompanied by any illustrations The first illustrations of basidia showing the exact position and size of the water-drops are contained in my paper entitled : " Die Erzeugung und Befreiung der Sporen bei *Coprinus sterquilinus*," *Jahrb. f. wiss. Bot.*, Bd. LVI (Pfeffer-Festschrift), 1915, pp. 299–329, Taf. II and III. This paper, written for a volume celebrating Pfeffer's seventieth birthday, was sent to Germany in July, 1914, a fortnight before the outbreak of the war.

autumn (Fig. 1). Its basidia are provided with two long slightly divergent sterigmata which project into the air above the gelatinous matrix in which the bodies of the hymenial cells are embedded. In order to watch the discharge of the spores in this species, I proceeded as follows. Some fresh fruit-bodies were gathered in a wood at Winnipeg and were allowed to dry in the laboratory. A few days afterwards some of them were revived by giving them access to water without their being submerged. New sterigmata and spores were quickly produced. A single small fruit-body was placed horizontally on a glass slide and covered with a cover-glass. The edge of the cover-glass which was raised above the glass slide by the thickness of the fruit-body, *i.e.* by about 1 mm., was then sealed round with vaseline. Thus the fruit-body came to lie in a small chamber containing moist air. On examination with the microscope, a number of sterigmata and spores could be seen projecting near the top of the fruit-body in a horizontal direction. With a magnification of 440 diameters, I watched a spore come into existence as a tiny rudiment on the end of a sterigma, grow to full size, and be discharged (Fig. 2). The total length of time which was thus occupied by one spore was only 1 hour and 20 minutes, and by each of two other spores approximately 1 hour and 30 minutes. The stages in the development and discharge of the spores were recorded by means of *camera-lucida* drawings made at intervals. For the spore shown in Fig. 2 the successive intervals were each 10 minutes. In 40 minutes, the spore developed from a minute rudiment to full size (B, C, D, E, F). Then there was a pause for 40 minutes. At the end of that time a tiny drop of watery fluid began to exude at the neck of the sterigma (G). The drop quickly grew in volume, and in about 10 seconds from its first appearance attained its maximum size (H). Immediately thereafter the spore was shot violently from its sterigma, and both spore and drop disappeared from view. Subsequent observations, soon to be described, taught me that,

FIG. 1.—Fruit-bodies of *Calocera cornea* on a piece of wood. Natural size. After Brefeld (*Untersuchungen*, Heft VII, Taf. 11, Fig. 14).

at the moment of discharge, the drop is carried with the spore. Hence, in Fig. 2 at I, the drop has been represented diagrammatically as

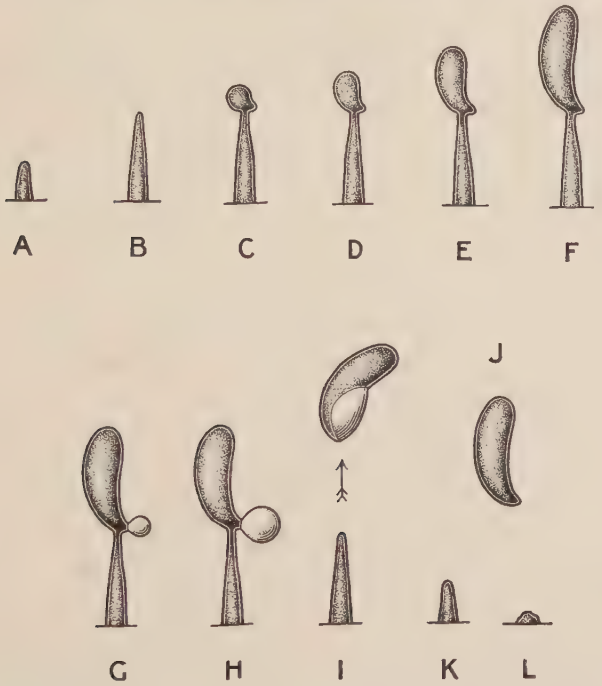


FIG. 2.—*Calocera cornea.* The development and discharge of a spore. A, an immature sterigma pushing out beyond the gelatinous matrix of the hymenium. B, a full-grown sterigma. C, D, E, and F, stages in the development of a spore, drawn respectively 10, 20, 30, and 40 minutes after the stage B. F, the full-grown spore on the end of its sterigma. G, the same spore 40 minutes later than the stage F: a drop of water is being excreted at the hilum. H, the same spore, about 6 seconds later than the stage G: the drop has attained its maximum size. I, a second or less later than H: the spore is being shot away from its sterigma. J, appearance of a spore after it has settled and after the drop which it carried has evaporated. K, a few minutes later than I: the sterigma sinking back into the hymenium. L, remains of the collapsed sterigma, a few minutes after the stage K. Magnification, 1,740.

clinging to the discharged spore. The sterigma, a few minutes after losing its spore, gradually contracted and was finally drawn down to the general level of the hymenium where it became lost to view (K, L).

The foregoing observations teach us: (1) that in *Calocera*

cornea the spores develop and are discharged with hitherto unsuspected rapidity, (2) that the excretion of a water-drop precedes violent spore-discharge, (3) that there is no drop left on the sterigma after discharge, and (4) that a newly-developed sterigma collapses a few minutes after discharging a single spore and, therefore, that a sterigma does not produce any more spores than one.

A spore of *Calocera cornea*, when coming into existence, arises obliquely and not directly at the end of the sterigma, as may be seen in Fig. 2 at C. The result of this is that a hilum is formed which projects toward the axis of the basidium-body. The excretion of the drop of water always takes place from the hilum. It therefore seems probable that the hilum is morphologically and physiologically of considerable importance. It is evidently a structure which is specialised for the rapid excretion of water, and it doubtless plays a very important rôle in bringing about spore-discharge.

In different species of Hymenomycetes, the interval of time between the moment when a spore begins to develop on the end of the sterigma and the moment of discharge is by no means constant, as will be shown by data given in the next Chapter. For the present it is sufficient to remark that this interval, whilst very short for *Calocera cornea*, is still shorter for certain other Hymenomycetes. Indeed, in some species, *e.g. Collybia velutipes* and *Dacryomyces deliquescens*, it is reduced to even less than one hour.

The Water-drop.—The excretion of a water-drop just before spore-discharge occurs not only in *Calocera cornea* but in numerous other, and probably in all, species of Hymenomycetes. Among some fifty species in which I have observed it may be mentioned those given in the Table on the opposite page.

The species in this list are fairly representative of the Hymenomycetes in general. They are sufficient to show that drop-excretion before spore-discharge is the rule in this great group.

With the high power of the microscope (magnification usually 440) I have watched hundreds of spores leave their sterigmata in different species, and never once, since I became acquainted with the excretory process, have I watched for the preliminary water-drop in vain.

In order to observe individual spores leaving their sterigmata

in one of the Agaricineae, my mode of procedure was as follows. A gill was removed from a living fruit-body, placed flat on a glass slide, and then covered with a cover-glass. No mounting fluid was used. The upper hymenial layer was then looked over with the low power of the microscope. Often a basidium was observed to have only three or two spores left upon it. The high power

Hymenomycetes Excreting a Liquid Drop at the Spore-hilum before Spore-discharge.

Family.	Order.	Species.
Tremellineae	Auricularieae	Hirneola auricula-judae
		Exidia albida
	Dacryomyceteae	Dacryomyces deliquescens
		Calocera cornea
Thelephoreae		Stereum hirsutum
Clavarieae		Clavaria formosa
Hydneae		Hydnum imbricatum
		Hydnum ferrugineum
Polyporeae		Polyporus squamosus
		Polystictus hirsutus
Agaricineae	Leucosporae	Collybia velutipes
		Lepiota cepaestipes
	Porphyrosporae	Psalliota campestris
		Stropharia semiglobata
	Ochrosporae	Galera tenera
	Rhodosporae	Claudopus nidulans
		Entoloma prunuloides
	Melanosporae	Coprinus atramentarius
		Coprinus comatus
		Anellaria separata
		Panaeolus campanulatus
		Psathyrella disseminata

was then applied, and such a basidium watched intently. The remaining spores, as a rule, were then seen to be discharged successively at intervals of a few seconds or minutes. Sometimes my attention was directed to a basidium with four apparently ripe spores upon it. Occasionally all four spores were then seen to be discharged one after the other. For *Hirneola auricula-judae*, *Stereum hirsutum*, and *Polystictus hirsutus*, sections through the hymenium were employed. In these sections the basidia were seen in side view.

When the upper hymenial surface of a gill which has been mounted in the manner just described is observed with the

microscope, the spores are seen to be in groups of fours, each group corresponding to a subjacent basidium. The drop of water, which

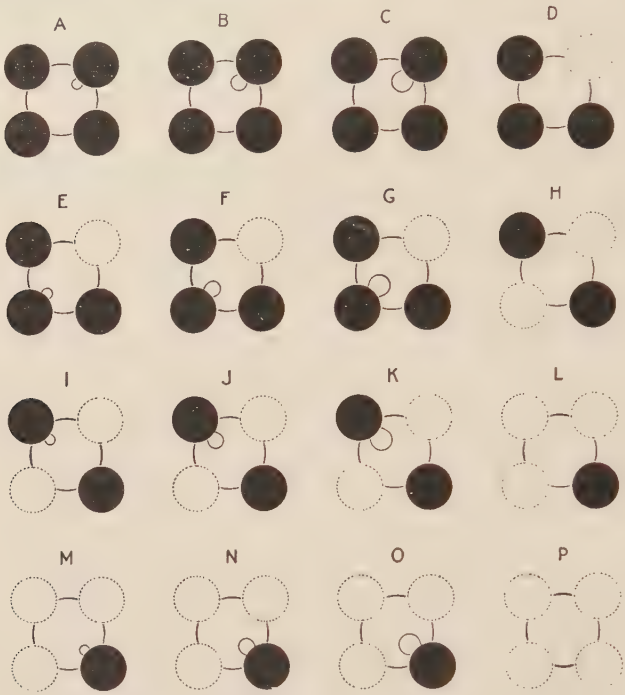


FIG. 3.—*Psalliota campestris*. Diagrammatic representation showing the successive discharge of the four spores from a basidium, as seen from above. A–D, stages in the discharge of the first spore; E–H, of the second; I–L, of the third; and M–P, of the fourth. A, a drop of water has just begun to be excreted where the right-hand top spore joins its sterigma. B, about two seconds later: the drop has grown. C, about three seconds after B: the drop has attained its maximum size. D, a fraction of a second after C: the spore has disappeared carrying the drop with it; the old position of the spore is represented by a dotted circle. Similar explanations apply to the other three horizontal lines of sketches, each of which represents the discharge of a single spore. The pause between the stages D and E, H and I, and L and M, was in each case a few minutes. All the stages from A to P were passed through in about 10 minutes. Magnification, 1,320.

is excreted a few seconds before a spore is to be discharged, always arises at the hilum of the spore, *i.e.* at the junction of the spore with its sterigma. Now the hilum always faces toward the longitudinal axis of the basidium-body. Hence the water-drop

faces in this direction also. For *Psalliota campestris*, the sequence of events for a single basidium during spore-discharge is represented semi-diagrammatically in Fig. 3. The hilum of the first spore to be discharged (A) excretes a drop of water which quickly grows to its maximum size (B and C). At this stage the spore is shot away and, at the same moment, the water-drop disappears (D). After a short interval of time, a few seconds or minutes, another spore is shot away (E, F, G, and H); then, after another interval, a third (I, J, K, and L); and finally a fourth (M, N, O, and P). For each spore, as is shown in the Figure, discharge is preceded by the excretion of a drop. A side view of a basidium, showing stages in the discharge of the last two spores, is given in Fig. 4. The interval between the moment when a water-drop first becomes noticeable and the moment of spore-discharge was observed to be about 5 seconds.

Not infrequently, soon after a drop has begun to form at the base of one spore, another drop begins to form at the base of a second spore, and so on. Thus in some basidia one may see two, three, or even four drops in course of growth at one time. The almost simultaneous production of three such drops is shown in Fig. 5. The relative ages of the drops are directly proportional to their size. Thus, at C, the drop on spore No. 1 began to be excreted before that on spore No. 2, and that on spore No. 2 before that on spore No. 3. The sterigma which begins to produce its drop first shoots off its spore first, and so forth. When the drops on a basidium appear almost simultaneously, the four spores are shot off their sterigmata in close succession. A basidium therefore sheds its four spores, after spore-discharge has begun, much more quickly when the sequence of events is as represented in Fig. 5 than when it is as represented in Fig. 3.

The size of the drop excreted before spore-discharge is very constant in the fruit-bodies of any one species, but in different species it varies considerably. However, it bears a certain relation to the size of the basidia and of the spores. The following Table shows the relation between the size of the spores and that of the drops in two species. The fourth column gives the number of seconds taken for the growth of a drop before spore-discharge.

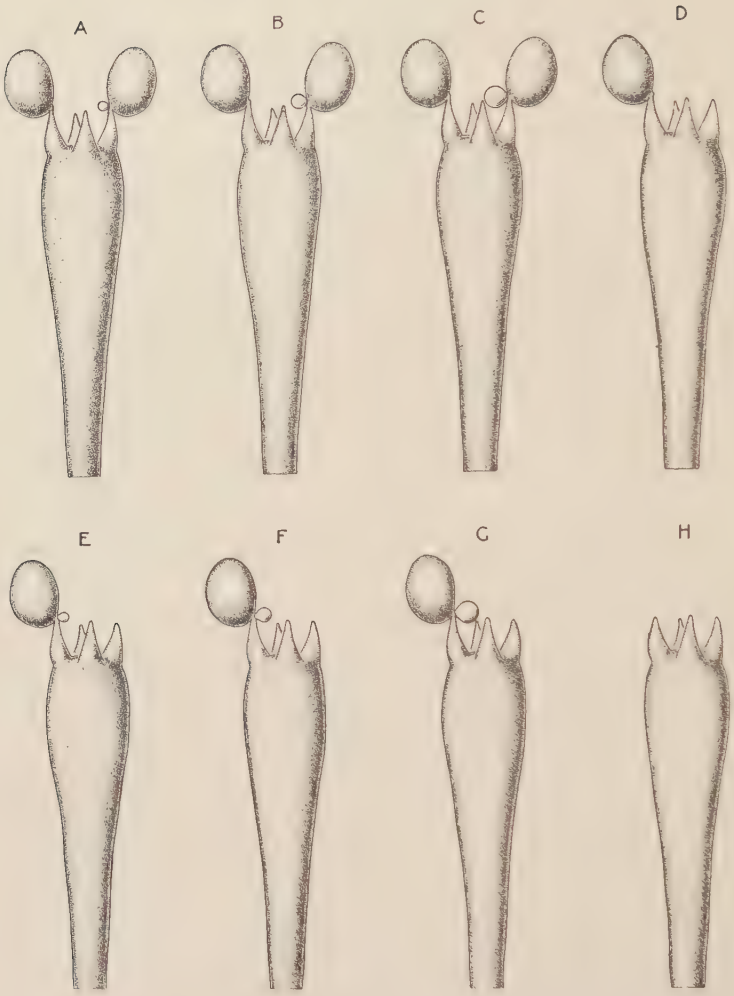


FIG. 4.—*Psalliota campestris*. The discharge of the third and fourth spores from a basidium as seen in lateral view. A–D, stages in the discharge of the third spore; E–H, of the fourth. A, a drop of water has just begun to be excreted at the hilum of the right-hand spore. B, about two seconds later than A: the drop has grown. C, about three seconds later than B: the drop has attained its maximum size. D, a fraction of a second later than C: the spore has been shot away and has carried the drop with it. Between D and E there is a pause of several minutes. E, F, and G show the growth of the water-drop at the hilum of the fourth spore, whilst H shows the appearance of the basidium after the fourth spore has been shot away. Magnification, 1,320.

Size and Rate of Growth of the Water-drop.

Species.	Maximum Diameter of the Water-drop in μ.	Size of Spores in μ.	Time taken for the Growth of the Drop in Seconds.
Coprinus sterquilinus . .	5	18–20 × 11–12	15–30
Psalliota campestris . .	2–3	9 × 5·5	5

At the moment when a spore is suddenly shot away from its basidium, so far as I have been able to observe, there is no

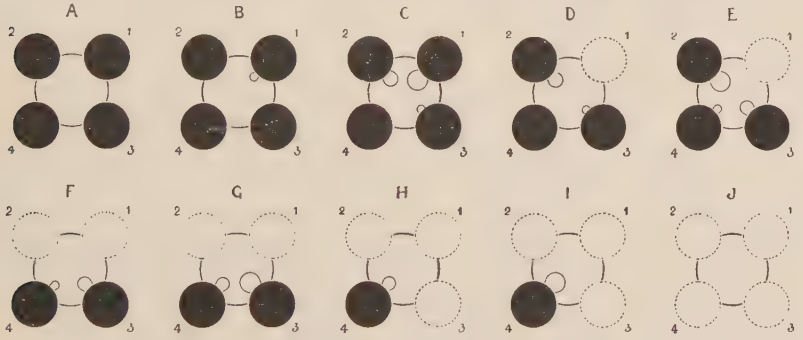


Fig. 5.—*Psalliota campestris.* Diagrammatic representation showing the discharge of four spores in rapid succession from a basidium as seen from above. The dotted circles show the positions of spores which have been shot away. The spores are discharged in order according to their numbers 1, 2, 3, and 4. The times of each stage, taking the stage A as the zero of the time scale, are approximately as follows: B, 2 seconds; C, 7 seconds; D, 7 seconds; E, 10 seconds; F, 10 seconds; G, 13 seconds; H, 13 seconds; I, 16 seconds; and J, 16 seconds. Thus all the spores are shot away in a quarter of a minute; but the discharge is rarely so rapid as this. Magnification, 1,320.

contraction of the basidium as a whole. Even when all four spores have just been discharged, the basidium appears to have just as large and turgid a body as before discharge began (*cf.* Fig. 4). It is evident that the spores are not squirted away from the basidium by the basidium-body contents and, therefore, that the mechanism of discharge is not analogous to that employed for the discharge of spores from the explosive asci of the Ascomycetes or for the discharge of the sporangium from the sporangiophore of Pilobolus.

For some time after beginning to observe the excretory phenomenon in connection with spore-discharge, I was puzzled as to what becomes of the drop at the moment when the spore is shot

away. There were three obvious possibilities. Firstly, the drop might run down the sterigma and spread itself over the basidium-body; secondly, the drop might become divided, part of it remaining on the sterigma and part of it being carried away by the spore; and, thirdly, the drop might be entirely carried away by the spore. Against the first two suppositions could be urged the fact that no trace of the drop is ever to be seen on the sterigma or basidium-body immediately after a spore has been discharged. On the other hand, it was observed that when spores are allowed to fall on to a glass slide placed beneath a fruit-body one cannot observe that, immediately they come to rest, they are enveloped in a liquid film. Close observation, however, has convinced me that the spores do carry away the drops with them. Evidence of this fact was obtained for *Entoloma prunuloides* in the following manner. Two basidia were found near to one another in the relative positions shown in Fig. 6 at A. After one of the basidia had shed three of its spores, I watched the fourth intently (B). Quickly a drop of water exuded from the hilum of the spore and in 5–10 seconds attained its maximum size (C). Then the spore was shot away and the sterigma was left vacant (D). The flight of the spore, as is usual in such observations, could not be followed with the eye. However, at the moment of discharge, the spore

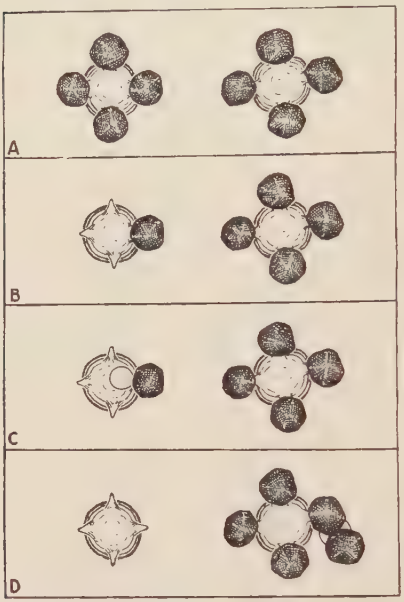


Fig. 6.—*Entoloma prunuloides*. Proof that the water-drop is carried with the spore. A, two adjacent basidia on a living gill seen from above. B, the left-hand basidium has discharged three of its spores. C, at the base of the fourth spore a drop of water has been excreted and has attained its maximum size. D, the spore has been shot upwards and has fallen upon one of the spores of the right-hand basidium. The drop of water which the discharged spore has carried away has run between the two spores. Magnification, 660.

fell upon one of the spores of the other basidium and stuck to it; whereupon I saw that a drop of water instantly ran from the discharged spore toward the undischarged, and became held by adhesion between the two (D). In a few seconds the drop spread itself more widely over the spores, and then disappeared, doubtless by evaporation. This observation leaves in my mind the conviction that the drop, which I had seen on the hilum before discharge, had been carried by the spore during its flight.

Observations similar in their nature to that just recorded I have occasionally made when studying spore-discharge in other species, *e.g. Coprinus sterquilinus*, *Psalliota campestris*, and *Galera tenera*. In each of these a spore, after being shot upwards from the horizontal hymenium, fell on to one of the basidia or paraphyses and, at the moment of settling, was seen to have a drop of water on its upper side. The drop in each case was approximately of the same size as that which normally is excreted at the hilum. In a few seconds it disappeared, partly by spreading slowly around the spore and, doubtless, partly by evaporation.

After making the occasional observations on the carriage of the drop just described, I devised an experiment which, provided living fruit-bodies are available, can be set up at any time and the results of which are sufficient to prove that the hilum-drop is carried by the spore in any hymenomycetous species whatsoever. The arrangement of the apparatus and the mode of observation for *Nolanea pascua* were as follows.

A compressor cell, like that shown in the first illustration of Chapter II, was used as a moist chamber to contain a piece of a gill with a developing hymenium.[1] A very tiny drop of water was placed on the base of the cell, and then a piece of a living gill dissected from a just-gathered fruit-body of *Nolanea pascua* was laid flat over the drop. The drop spread out into a fine film between the under side of the piece of gill and the glass. The lid of the compressor cell was then pushed down over the box until it was nearer to the tops of the upward-projecting spores than 0·1 mm., *i.e.* so that the under side of its cover-glass would form a target

[1] A similar compressor cell was used for various investigations recorded in 1909 in Volume I. *Vide* vol. i, Fig. 58, p. 167.

which would be struck by the spores when they were shot upwards. Then, using the high-power objective of the microscope with a magnification of 440 diameters, I concentrated my attention for some hours on the largest, most angular, and pinkest of the spores, *i.e.* the ones which seemed most mature. These, on being discharged, instantly stuck to the cover-glass just above the sterigmata upon which they had been developed. I observed that every spore which struck the cover-glass target was accompanied by a drop of water, which ran between the under surface of the cover-glass and the spore. Once, by carefully focussing a ripe spore seated upon its sterigma, I observed the excretion of a small drop at the hilum of the spore, saw the drop grow for about 4 seconds to nearly full size (Fig. 7, A), then instantly raised the tube of the microscope so as to focus the lower surface of the cover-glass just above the spore, and then had the satisfaction of seeing the spore and the drop strike the cover-glass together and remain adhering to one another and to the cover-glass (B). Here, therefore, the drop was seen attached to one and the same spore both before and after discharge. Immediately after the spore had struck the target, I focussed the microscope upon the sterigma from which the spore had been shot and found it to be free from any drop. These

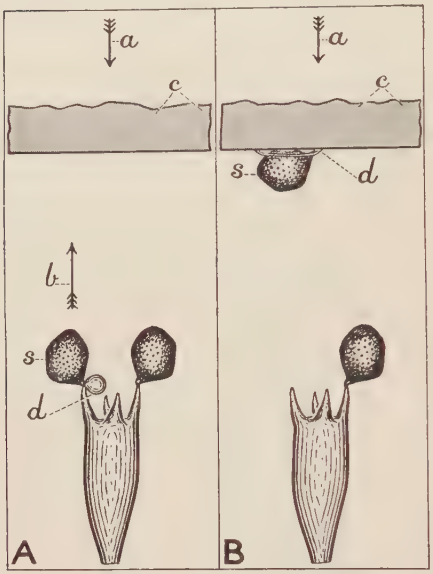


FIG. 7.—Diagram to illustrate the method used for observing the discharge of a spore from a gill of *Nolanea pascua*. A: the basidium shown was in the upward-looking hymenium of a gill contained in a closed compressor cell. The microscopist looked through the cover-glass *c* in the direction shown by the arrow *a* and observed the excretion of the drop *d* at the hilum of the spore *s* which was destined to be shot in the direction shown by the arrow *b*. He then raised the plane of focus to the under surface of the cover-glass *c* and, within two seconds, as shown in B, saw the spore *s* with its attached drop *d* strike and stick to the cover-glass.

observations permit only of one inference and that is that the drop excreted at the spore-hilum is carried by the spore in its flight through the air.

The carriage of a drop of water by every spore which has just been discharged helps to account for the extraordinary adhesiveness of hymenomycetous spores when they are newly liberated. They stick to any surface which they happen to touch. After they have settled, if the air is not saturated with moisture, owing to the very small amount of water which they contain and have adherent to them, they quickly dry up. Whilst drying they press themselves more and more firmly to the substratum on which they lie. If they have settled on a glass slide and have dried there, it often happens that, if one attempts to remove them with a needle, they do not come away without breaking. Probably, when a moist spore settles on a glass slide, owing to capillary attraction, a little water passes from the spore so as to lie between itself and the slide. Assuming the existence of this water, it seems likely that, on its evaporating, it drags down the smooth-coated spore to the slide in such a manner as to flatten it out and thus to increase the area of contact.

Sometimes the excretion of water from the hilum takes place in an abnormal manner. Several times I have noticed that, when a gill of a Mushroom which has been kept under moist conditions is mounted in air under a cover-glass, certain basidia which at the ends of their sterigmata bear partly or fully grown yet immature spores excrete water in abundance. The water arises from the hila of the spores in the form of drops (Fig. 8, A). These at first resemble the drops which are normally produced just before spore-discharge, but they continue to increase in size until they meet and fuse (B, C). One large drop is then held between the two young spores (D). Finally, the drop becomes so large that it runs down between the two sterigmata and disappears by moving on to the surface of the hymenium. A second instance of abnormal excretion of water by a basidium is afforded by the following observation upon *Lepiota cepaestipes*. A transverse section was taken through some gills and was mounted in water under a cover-glass. The water, owing to the imprisonment of air, did not invade every

interlamellar space. Into one such air-filled space the basidia were projecting freely. One of the basidia bore four spores which were just beginning their development (Fig. 9, A). From the hilum of one of the spores a tiny drop of water was excreted (A), which quickly grew larger (B), until in a few minutes it had reached a relatively enormous size (C). The drop thus precociously excreted was larger in volume than the basidium itself. The basidium did not alter in size during the excretion. We must therefore suppose that as much water flowed into the basidium from neighbouring

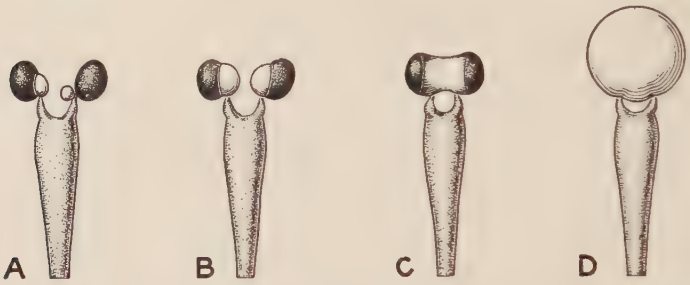


Fig. 8.—*Psalliota campestris* (cultivated form). A, B, C, and D, stages in the abnormal excretion of water from the hila of two spores of a basidium. A, one drop is of normal size, the other larger than normal; the latter has stepped up on to the side of the spore. B, the drops have grown larger and both are now adherent to the sides of the spores. C, the drops have touched, and have united to form one drop which has dragged the spores toward one another. D, the drop has continued to increase in size and has now become globular, thus enclosing the two spores. Magnification, 880.

cells as was excreted at the top of the sterigma. Normal discharge of a spore of *Lepiota cepaestipes* is shown in Fig. 9 at D, E, and F. At E the drop has reached its maximum size. The next moment the spore is discharged and the sterigma is left vacant, as is represented at F.

Certain other remarks upon the abnormal excretion of water by basidia just prior to spore-discharge will be made in Volume IV in the course of a comparison of the discharge of basidiospores in the Hymenomycetes and the Uredineae.

The Chemical Constituents of the Drop.—The largest drops which I have yet seen are those excreted from the hila of the large spores of *Coprinus sterquilinus*, but their diameter is only 0·005 mm. They are so excessively minute and have such a brief existence

that, at present, it seems impossible to subject them to chemical analysis. However, a drop doubtless consists chiefly of water: for it has a perfectly rounded form during its excretion, behaves like a drop of water when touched, on contact with another similar drop unites with its fellow to form a single drop, refracts light like water, is colourless and transparent, and undergoes rapid evaporation in unsaturated air. But it would be rash to assert that the drop consists only of water in view of the investigations by Knoll [1] upon the supposed drops of water excreted from the ends of the pileal hairs of *Coprinus ephemerus*, *Psathyrella disseminata*, etc., various cystidia, and the sporangiophore of Pilobolus. Knoll discovered that all these drops contain a colloidal constituent which appears to be mucilage. This he proved by observing the irregular form of the drops when contracting during evaporation, the solubility of the drops in water and their insolubility in alcohol, etc.; and he came to the conclusion that the mucilage is formed by local mucilaginisation of the cell-wall. Knoll also showed that, as the drops dry up, crystals of calcium oxalate are often formed. This occurs for example in the drops on the ends of the cystidia of *Inocybe trichospora*. In view of these observations it may well be asked: do the drops excreted on the hila of the spores of Hymenomycetes contain mucilage? By analogy I strongly suspect

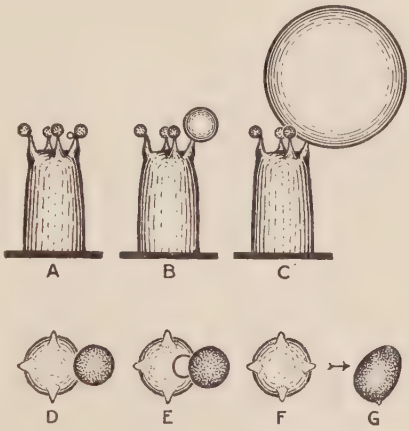


FIG. 9.—*Lepiota cepaestipes*. A–C, abnormal excretion of water from the hilum of a very rudimentary spore. A, first appearance of a drop at the hilum of the right-hand spore. B, the drop has grown and has enclosed the spore. C, the drop has now attained its maximum size. D–G, normal discharge of a ripe spore as seen from above. D, one spore is left on the basidium. E, a drop of water has been excreted at the hilum and has attained its maximum size. F, the spore has been shot upwards and has fallen at G. The drop of water which was carried with the spore has evaporated and is not represented. Magnification, 990.

[1] F. Knoll, "Untersuchungen über den Bau und die Function der Cystiden und verwandter Organe," *Jahrb. f. wiss. Bot.*, Bd. L, 1912, pp. 453–501.

that they do, but so far I can produce no evidence in support of this supposition. It is not unlikely that a hilum-drop is only excreted when a minute portion of the wall of the hilum changes into mucilage, and that the mechanism of excretion is therefore similar to that for the excretion of drops on the pileal hairs of *Coprinus ephemerus*, the cystidia of *Inocybe trichospora*, and the sporangiophore of Pilobolus. It is also possible that the drops in addition to water and mucilage contain crystalloidal bodies such as calcium oxalate, etc., but here again there is at present no evidence to support such a supposition. We may conclude, therefore, that the drops consist chiefly of water but that, judging by analogy, it is probable that they contain other substances in solution.

Stokes' Law.—In the first volume I gave an account of some experiments upon falling spores which were made for the purpose of testing Stokes' Law.[1] My calculations, which were based on measurements of the density, radius, and rate of fall, showed that the spores of *Amanitopsis vaginata* fall 46 per cent. more rapidly than they should do according to Stokes' Law. The Law was therefore not verified in detail. The observations on the rate of fall were made upon spores which were just passing out from between two gills in a small compressor cell, the air of which was saturated with water vapour. At the time when my experiments were made, I did not know, as I do now, that a tiny drop of water is carried away upon the exterior of each spore. Now, according to Stokes' Law, the rate of fall of a minute sphere varies directly as the square of the radius. The addition of a water-drop to a spore increases its effective radius and therefore also its rate of fall. It seems to me, therefore, that the excess rate of fall which I observed was, in part at least, due to the water-drop which I had not perceived and which my calculations therefore did not take into account. With a correction of the radius based on the size of the drop carried away by each spore, my experimental results could be brought into closer agreement with Stokes' Law. To continue my investigations in this direction, however, has become unnecessary on account of the fact that, since my observations were published in 1909, Zeleny and M'Keehan, using a method far

[1] Vol. i, 1909, p. 173.

more delicate than my own, have shown that Stokes' Law for the fall of small spheres of a certain range of size in air *is* approximately true.[1] These authors measured the density, radius, and rate of fall of minute spheres of wax, mercury, and paraffin, which were obtained by spraying. The rate of fall, as actually observed for spheres about the size of spores, was found to be in almost exact accordance with the Law.

Millikan,[2] who has contributed much to the recent upbuilding of the atomic theory of electricity, by employing a method even more delicate than that of M'Keehan and Zeleny has shown that Stokes' Law, while true within 2 per cent. for spheres with a diameter of 0·001 cm. or 10 μ, *i.e.* for spheres about the size of spores, becomes increasingly inexact for spheres of smaller and smaller diameter. Stokes' Law, in its original form, is represented by the following equation :

$$V = \frac{2}{9} \frac{\rho - \sigma}{\mu} g a^2$$

The Law, as corrected by Millikan, has the following form :

$$V = \frac{2}{9} \frac{\rho - \sigma}{\mu} g a^2 \left(1 + \frac{b}{pa}\right)$$

where V = the terminal velocity,
ρ = the density of the falling sphere,
σ = the density of the medium,
g = the acceleration due to gravity,
a = the radius of the falling sphere,
μ = the viscosity of the medium,
p = the pressure of the gaseous medium,
b = a constant (according to Millikan = $6{\cdot}25 \times 10^{-4}$ when p is measured in centimetres of mercury).

Zeleny and M'Keehan measured the rate of fall of the dry spores of Lycopodium, Lycoperdon, and Polytrichum, with the result that the spores were found to fall much more slowly than they should do according to Stokes' Law. Thus the spores of

[1] Zeleny u. M'Keehan, "Die Endgeschwindigkeit des Falles kleiner Kugeln in Luft," *Physikalische Zeitschrift*, Bd. XI, 1910, pp. 78–93.

[2] R. A. Millikan, *The Electron*, Chicago, 1917, pp. 88–122.

Lycopodium fell with a velocity which was only about one-half of that required by theory. The fraction for the spores of Lycoperdon was about four-sevenths and that for Polytrichum about two-thirds. Zeleny and M'Keehan were unable to account for the want of agreement between fact and theory in the fall of dry spores. There is therefore room for further experiments in this direction. It is of some biological advantage that spores should fall but very slowly in still air. Possibly dry spores have some peculiarity in their construction, yet to be found out, which serves in a special manner to reduce the rate of fall to a minimum.

The Mechanism of Spore-discharge.—The exact nature of the mechanism by which the spores are shot violently from their sterigmata still remains a mystery. In Volume I, I showed that the mechanism is not like that of asci: the basidium does not explode and squirt the four spores away. I suggested that the spores are discharged in the same manner as those of certain Entomophthoraceae. In these fungi a double membrane is formed between the spore and its basidium. At the moment of discharge these two membranes separate from one another, and each, owing to the osmotic pressure in the spore and in the basidium, suddenly becomes convex towards the other. The spore is thus jerked away. However, I pointed out that, for the Hymenomycetes, no one has ever seen any double membrane separating a spore from its sterigma. The neck of a sterigma where it joins the spore has so small a diameter that an optical difficulty prevents one from directly seeing what it contains.[1]

I am now inclined to believe that no such double membrane

[1] W. E. Hiley, in describing the hymenium of *Fomes annosus* (*The Fungal Diseases of the Common Larch*, Oxford, 1919, pp. 103–104), says: "Each spore is attached to the basidium by a very thin extension of the latter called a *sterigma* (Fig. 41, B, *st*), and when ripe the spore which develops at its extremity is cut off from the sterigma by a transverse septum . . . the ejection is accomplished by the splitting of the septum between the spore and the sterigma"; and in his Fig. 41 he shows a diagram of a sterigma with a septum across the sterigmatic neck. Hiley's account of the septum in *Fomes annosus* appears to be based on theory rather than on actual observation; and his diagram is evidently imaginary, for the sterigma is represented as being curved convexly toward the basidium-axis, instead of concavely as it should be, with the result that the attachment of the sterigma to the hilum of the spore is incorrectly illustrated.

exists as that to which reference has just been made. Using a fruit-body of *Coprinus sterquilinus*, I tried the effect of breaking off spores from their sterigmata at a stage when the spores had attained full size but were only half-ripened. The protoplasm was still flowing into the spores, for the basidia had become only about half-emptied. I found that a half-ripened spore, isolated from its sterigma in the manner indicated, remained quite turgid although the canal leading into it through its membrane at the hilum was still open so far as the cell-wall was concerned. Plasmolysis could be effected readily with a solution of 10 per cent. potassium nitrate. These observations seem to show that the canal has so small a diameter that the osmotic pressure of the cell-sap is insufficient to press the protoplasmic contents of the spore through it. It is also very probable that, when a spore is removed from a sterigma, the opened sterigmatic canal is too narrow to permit of the osmotic pressure of the basidium driving the basidial contents out through it. We may therefore draw the conclusion that a double wall is unnecessary to close the ends of a spore and its sterigma at the moment of spore-discharge ; for, even if they remain open, the cell-contents cannot be forced out through them.

Assuming tentatively that no double membrane is formed between a ripe spore and its sterigma, and that, when a spore is discharged, the end of the sterigma is simply broken across, what can be the nature of the force which causes spore-projection ? As yet I can give no satisfactory answer to this question. The remarks which follow are intended to stimulate further investigation which may lead to a solution of the problem. Before assuming the presence of a double membrane between spore and sterigma at the moment of discharge, we ought to try to solve the problem by taking into account all the following facts :

(1) The existence of a structure called the hilum—a tiny blunt process projecting from the base of the spore. This is always developed and is the point where a spore separates from the sterigma. It is therefore probably the seat of the force which brings about discharge.

(2) The extreme narrowness of the necks of all sterigmata. The

diameter varies from 1 μ in the large basidia of *Coprinus sterquilinus* to about 0·25 μ in species with very minute basidia. In *Psalliota campestris* the diameter is about 0·5 μ.

(3) The successive and not simultaneous discharge of the four spores.

(4) The maintenance of the turgidity of the basidium-body during the successive discharge of the spores.

(5) The non-collapse of the sterigma immediately after it has discharged its spore.

(6) The excretion of a drop of water at the hilum as an invariable preliminary to spore-discharge.

(7) The carriage of the water-drop with the spore when this is shot away.

(8) The fact that a spore does not burst but remains turgid when it is violently broken off its sterigma, at a time when the canal through the spore-membrane leading down to the sterigma is still open.

(9) The minute diameter of the canal through the spore-membrane and sterigma.

It may be regarded as certain that the mechanism for the discharge of each spore is localised at the end of each sterigma, and that the four sterigmata, so far as spore-discharge is concerned, act independently of one another. It is at the hilum that the force applied in the discharge of a spore becomes developed and effective. The hilum, since it excretes a drop of water of relatively considerable size in from 5 to 10 seconds just before spore-discharge, evidently is able to control the passage of fluid through its membrane.

It is possible that a spore is shot from its sterigma by hydrostatic pressure. It may be that, at the hilum, water is pumped into a small place by the protoplasm and that, when the hydrostatic pressure is increasing in this small space, a certain amount of the water escapes in the form of the drop which has already been described. Possibly the drop weakens the cell-wall on which it rests by acting chemically or physically upon it. We may then suppose that, when the membrane has thus been

weakened up to a certain point, the hydrostatic pressure in the hilum causes an explosion, so that the spore is shot from its sterigma. The explosion, owing to its localisation at the top of the sterigma, does not involve the whole basidium. Further, we must suppose that the amount of water liberated by the hydrostatic explosion at the tip of the sterigma is so minute that, even with a microscope, there is little hope of our ever perceiving it.

I do not feel that this theory is altogether satisfactory, but have brought it forward as a basis for further discussion of the whole question. The absolute constancy of the preliminary excretion of a drop seems to make it certain that the drop plays an essential part in preparation for spore-discharge. I have assumed that the drop is useful in that it acts upon the hilum-membrane from without and thus weakens it prior to discharge. However, in Pilobolus and the asci of Ascomycetes, the membrane which breaks is weakened from within and no drop analogous to that excreted by the hilum of the basidium is ever produced. No support for my supposition as to the function of the drop can be obtained from the Phycomycetes or the Ascomycetes.

I have suggested that the drop acts either chemically or physically on the wall on which it rests and thus weakens it in preparation for spore-discharge. Possibly, however, the growth of the drop only accompanies such a weakening of the wall and is not the cause of it. The excretion of drops from the pileal hairs of *Coprinus ephemerus*, *Psathrella disseminata*, the cystidia of *Inocybe trichospora*, and the sporangiophore of Pilobolus, etc., has, as already pointed out, been shown by Knoll to be accompanied by the mucilaginisation of those small portions of the outer part of the cell-wall from which the drops arise. Judging by analogy, therefore, it seems not only possible but even probable that, whilst the hilum-drop is being excreted, the wall joining the sterigma and spore is undergoing change—perhaps mucilaginisation—and is thus becoming weakened in preparation for spore-discharge; and that, as soon as this weakening has attained a sufficient degree, the explosive force in the sterigma causes the spore to be shot away. It may be that the supposed mucilage, as it is being formed, pulls water from the sterigma by its force of imbibition and thus

forms the drop. Possibly, therefore, the formation of a drop is merely the outward and visible sign of the weakening of the cell-wall which takes place in preparation for spore-discharge, and is nothing more than a necessary physical accompaniment of an alteration in the chemical or physical condition of the cell-wall.

The drop of water is always carried away by the spore at the moment of its discharge. This is not surprising since the hilum which excretes the drop is part of the spore. From the physical point of view it is therefore clear that the drop serves to increase the mass of the projectile. This increase of mass doubtless permits of the spore being shot further from the basidium than it would be without the addition of water to it. After a spore has reached an interlamellar space and begins to fall vertically, the water-drop very quickly dries up, so that it does not hasten the fall of a spore to the ground. One must admit, therefore, that the drop of water is useful in that, by increasing the projectile-mass, it assists the sterigma in its work of shooting the spore to a safe distance from the hymenium before the spore begins to fall vertically. The fluid which in Pilobolus clings to the sporangium, and which in Empusa, Ascobolus, and Peziza clings to the spores, is certainly of considerable importance as a means of increasing the projectile-mass, and thereby of increasing the distance to which the mass can be shot.[1] I am inclined, however, to think that, while the drop excreted at the hilum of the spore in Hymenomycetes does increase the mass of the projectile and thus permits of the projectile being shot a little further than it otherwise would be, this is only an incidental advantage and does not give us a clue to the primary significance of drop-excretion.

It may be that the force of surface tension is used in some way to effect spore-discharge; but exactly how I cannot satisfactorily explain. Possibly we have an entirely new principle involved in the mechanism of spore-discharge in the Hymenomycetes which, when properly elucidated, will prove of the highest interest and once more show how organisms are able to avail themselves of the forces of nature in order to maintain their existence.

[1] *Cf.* vol. i, 1909, Part II, Chap. II, pp. 253–254.

Does a Basidium Produce more than One Generation of Spores?—Corda, in 1839, stated that in the Agaricini each sterigma produces several spores in succession, one after the other, in the same manner as the terminal branches of the conidiophores of certain Moulds.[1] Schmitz, in 1843, after studying the production of spores from the living hymenium of *Stereum hirsutum* (his *Thelephora hirsuta*), expressed the view that one and the same basidium can produce sets of four spores not merely once but many times.[2] Worthington Smith believed that the basidium of a Mushroom (*Psalliota campestris*) produces two generations of spores, first two spores on two sterigmata and then two more on two other sterigmata.[3] Recently, Istvánffi and René Maire have revived the theory of Corda and Schmitz. In order to explain some of the results of their nuclear studies, they have assumed that in some species a single basidium can produce more than one generation of spores. This assumption has been made by Istvánffi for *Hydnangium carneum*.[4] René Maire, in synthesising the results of his researches, states that in the normal types of Basidiomycetes the basidium produces a single generation of four spores, but that in Psalliota, Godfrinia, Cantharellus, Clavaria, Mycena, Geaster, etc., it produces either two, three, five, or six spores in a single generation, or two generations of four spores, or two generations of spores of unequal number [5]; and finally, in his chief conclusions as regards facts, he holds that in many species of Basidiomycetes the basidium can produce two generations of spores on the same sterigmata.[6] Here I wish to challenge Maire's conclusions in so far as they assume that the same basidium may produce more than one generation of spores. Maire worked on dead material. He fixed it, stained it, and cut it up with the microtome. He counted

[1] A. C. I. Corda, *Icones Fungorum hucusque cognitorum*, Prag, T. III, 1839, p. 43.

[2] J. Schmitz, "Beiträge zur Anatomie und Physiologie der Schwämme," *Linnaea*, Bd. XVII, 1843, p. 437.

[3] Worthington Smith, "Structure of the Common Mushroom," *Gardeners' Chronicle*, Oct. 1876, p. 456. The accompanying illustrations are certainly erroneous.

[4] Gy. von Istvánffi, "Ueber die Rolle der Zellkerne bei der Entwicklung der Pilze," *Ber. d. D. bot. Gesell.*, Bd. XIII, 1895, p. 464.

[5] René Maire, "Recherches cytologiques et taxonomiques sur les Basidiomycètes," *Bull. Soc. Myc. France*, T. 18, 1902, p. 187.

[6] *Loc. cit.*, p. 204.

the number of nuclei in the basidia and spores. Never once did he actually observe one and the same basidium in the living state produce more than one generation of spores. He deduced his conclusions from his nuclear studies. Now my experience, based upon extensive observations on the living hymenium, is that a basidium never produces more than one generation of spores and that, after producing a single crop of spores, its sterigmata and body quickly collapse. In writing of *Calocera cornea*, Maire states that the secondary (fusion) nucleus of the basidium divides to form either two or four daughter nuclei, and that in the latter alternative there are two generations of spores : each spore receives only one nucleus.[1] Now my observations on the fruit-bodies of *Calocera cornea*, which are epitomised in Fig. 2 (p. 7), go to prove that a sterigma, soon after shooting away its spore, collapses. This was observed for living basidia not once but several times. In no case did I see a sterigma produce two spores in succession. Direct observations, therefore, do not support Maire's assumption.

In the cultivated Mushroom (*Psalliota campestris*) and in *Coprinus bisporus* Lange, the basidia are disterigmatic and therefore produce only two spores at one time (Fig. 8, p. 18). In both these fungi, as I have observed by examining the living hymenium, there is only one generation of spores. In the Coprinus, each basidium, soon after shedding its spores, becomes involved in the upward moving zone of autodigestion and is therefore destroyed before there is any possibility of its producing a second generation of spores. In the Mushroom, shortly after a basidium has discharged the second of its two spores, its sterigmata collapse and its body shortens and sinks down into the hymenium. It can then be seen with two sterigmatic stumps at its outer end. In this condition it is no longer living. There is therefore not the slightest direct evidence to support the supposition that a basidium of *Psalliota campestris* ever produces two generations of spores.[2]

There is a relation between the volume of a basidium and the

[1] René Maire, *loc. cit.*, p. 78.

[2] The collapse of the bisporous basidia of the cultivated Mushroom takes place in exactly the same manner as that of the quadrisporous basidia of the wild Mushroom. The phenomenon of basidial collapse will be dealt with in more detail in later chapters, *e.g.* Chapter X.

total volume of the spores which it produces. In the cultivated form of *Psalliota campestris* the basidia are all of about the same size. Most of them produce two spores, but exceptions to this rule are not infrequent, for it is not difficult to find basidia which have but one sterigma and one spore only. The volume of the spore of a monosterigmatic basidium is twice that of one of the spores of a disterigmatic. A monosterigmatic basidium is equal in size to, and contains as much protoplasm as, a disterigmatic. There is therefore as much protoplasm available for the single spore of the first as for the two spores of the second. The sizes of the spores are evidently adjusted to the amount of protoplasm which they are destined to contain.

In most species of Hymenomycetes, the spores take several hours to mature after coming into existence. After they have grown to full size, all the protoplasm of the basidium-body, with the exception of a thin lining layer, flows into them. There is therefore none left over which might be used for the production of a second generation of spores. This is true for all basidia, so far as my observations go, whatever the number of spores which they produce. The whole mechanism of the basidium seems to me to be adapted for the production of a single generation of spores and no more.

The Sterigma and Spore-hilum in Hymenomycetes and Gastromycetes.—Throughout the Hymenomycetes, the sterigma is well developed and consists of a distinct, longer or shorter, gently curved, tapering, conical body. Moreover, in all the species of this great group, a hilum, from which a drop of water is exuded just before spore-discharge, comes into existence in the first stage of each spore's development. The hymenomycetous spore, when full-grown, has a long axis which is inclined at an angle of about 45° to the long axis of the subjacent sterigma. Where the basidium is quadrisporous, the four sterigmata are symmetrically spaced about the free end of the basidium, so that the distances between successive sterigmata are all equal. The spores are symmetrically arranged in the same manner and all their hila are turned inwards toward the basidium-axis. This beautifully symmetrical quadrisporous basidium is typical for the Hymenomycetes, and occurs

constantly in the vast majority of species, from Corticium to Coprinus, from Clavaria to Cortinarius, from Stereum to Schizophyllum, from Hydnum to Hygrophorus, and from Polyporus to Panaeolus. In the Tremellineae, which seem to form a link with the Uredineae, although the symmetry of the basidium is less striking than in the Thelephoreae, the Clavarieae, the Hydneae, the Polyporeae, and the Agaricaceae, the sterigmata and spore-hila are always well developed. In the non-tremelloid groups, a

FIG. 10.—*Scleroderma vulgare*, a gastromycetous fungus, lacking sterigmata, commonly found under Oak trees, etc. Photographed by A. E. Peck at Scarborough, England. Natural size.

few species have bisporous basidia and some others hexasporous; but, in these and all other exceptional species, the sterigma and hilum have the normal development, and the different sterigmata and spores are symmetrically arranged at the end of the basidium-body.

In the Gastromycetes, on the other hand, the basidium has no typical or almost constant form. The number of spores on an individual basidium varies much. Thus in *Scleroderma vulgare* the number is from 2 to 5, while in *Phallus impudicus* it is usually about 9, these being packed tightly together, side by side in a bundle at the end of the basidium. The spore-hilum is usually not (perhaps never) developed at all. One may look for it in vain,

for instance, in the two species already mentioned and in the various species of Lycoperdon. However, the most striking feature of the gastromycetous basidium is the variability of the sterigma. In some species, *e.g. Phallus impudicus* and *Scleroderma vulgare* (Figs. 10 and 11), the sterigmata are so exceedingly short that they only just suffice to attach the spores to the basidium-bodies from which they have been developed. In Lycoperdon, the sterigmata are usually long but extraordinarily thin. In *L. gemmatum* they are narrowly cylindrical in form and very variable in length and arrangement (Fig. 12). In *L. nigrescens* each basidium usually has four very slender sterigmata of about equal length, but the sterigmata break across and remain attached to the spores when these are set free. Furthermore, in Gastromycetes, *e.g.* Phallus, Scleroderma, and Lycoperdon, each spore is usually situated symmetrically upon the top of its sterigma instead of being laterally inclined. It will not be necessary here to give any further details of the structure of gastromycetous basidia. Enough has been said by way of illustration, and we may now ask the question: why are gastromycetous basidia so different from hymenomycetous? My own answer is as follows. *The typical sterigma* in association with the spore-hilum, such as we find generally in Hymenomycetes, is to be regarded as *an organ for the violent discharge of the spore which the sterigma develops.* This violent discharge of the spores, brought about by secret means by the sterigmatic guns, as I showed in Volume I, is of the very greatest importance to Hymenomycetes, in that it permits of the spores escaping from the hymenium into the air and thus becoming disseminated by the wind.[1] In Gastromycetes, on the other hand, the mode of spore-liberation is entirely different from

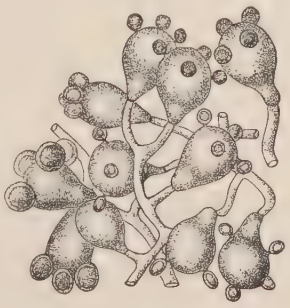


FIG. 11.—*Scleroderma vulgare*, one of the Gastromycetes. A piece of a mass of tangled basidia which fills each glebal chamber. The basidia lack sterigmata and the sessile spores are not violently discharged. After Tulasne, from von Tavel's *Vergleichende Morphologie der Pilze*. Highly magnified.

[1] *Researches on Fungi*, vol. i, 1909, pp. 133–134.

that of Hymenomycetes. The spores of gastromycetous fungi are produced in closed chambers within the fruit-body instead of on a free external hymenium. These chambers only open after all the spores have ripened, so that the spores are unable to escape one by one as they come to maturity. When the spores become enveloped in a sweet fluid, as in the Phalloideae, the agent for spore-dissemination is insects ; but, if the spores dry up and become powdery, as in Lycoperdon, the agent is usually the wind. In no species of Gastromycetes do the basidia discharge their spores directly into the air. Now, in the closed chambers of gastromycetous fruit-bodies, violent spore-discharge would not only be useless but might be positively harmful. Assuming that the Gastromycetes have been derived from the Hymenomycetes, it seems to me, therefore, that violent spore-discharge has become suppressed in the Gastromycetes. Assuming such suppression to have taken place, we may suppose that the well-developed sterigma, which, in association with the spore-hilum, had the function of violently propelling the spore in the ancestral Hymenomycetes, became useless during the development of internal hymenial chambers and, therefore, in the course of the evolution of the Gastromycetes, became either more or less suppressed or deformed. This degeneration of a once useful structure finds parallels in the reduction of the posterior pair of stamens in the flower of Salvia to functionless staminodes, in the suppression of the eyes but not the eye-stalks of certain American cave Crustacea, and in the almost total obliteration of the hind limbs of the Python.

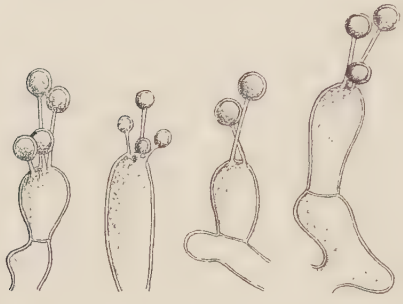


Fig. 12. — *Lycoperdon gemmatum*, a common Puff-ball. Basidia from the hymenial chambers of a fruit-body. The sterigmata are cylindrical in form and variable in length, number, and arrangement. The spores lack hila and are not violently discharged. After Ed. Fischer, from the *Pflanzenfamilien*. Highly magnified.

The degeneration of the typical basidium in cleistocarpous Basidiomycetes finds its parallel in the degeneration of the typical ascus in subterranean Ascomycetes. In Discomycetes, *e.g.* Peziza,

Otidea, Ascobolus, and Morchella, which are subaerial, the ascus-gun is beautifully perfected : it is drawn out into a long tube with the eight spore-projectiles arranged in a row just behind the gun's apex, the ascus-wall is very elastic, the gun explodes at its apex by the breaking away of a little lid, and the eight spores are shot violently forward to a distance of some two or three centimetres. The smoothness of the spore-walls permits of the projectiles passing out of the end of the ascus-gun with the least possible friction.[1] On the other hand, in some subterranean Tuberaceae, *e.g.* the well-known Truffles of the genus Tuber, where a violent discharge of the spores would no longer be of any biological advantage and does not take place, the ascus has lost its tubular form and is now oval or rounded, the spores are no longer arranged in a row one behind the other, the number of spores in each ascus is less than eight—usually two to four, the ascus-wall is not so elastic and does not open apically by a lid, and the spore-walls are no longer smooth.

A comparison of gymnocarpous with cleistocarpous fruit-bodies in Basidiomycetes and Ascomycetes thus compels us to conclude that the typical forms of the basidium and of the ascus are intimately associated with the efficiency of these cell-organs in the performance of one of their chief functions, namely, the violent discharge of the spores ; and, at the same time, it teaches us that where the function of violent spore-discharge has become lost both the basidium and the ascus tend to undergo a series of degenerative modifications in structure.

Balloons Falling from Rest or Fired from a Gun, Used to Illustrate the Movements of Spores.—It is impossible to observe the minute spores of the Hymenomycetes whilst they are being projected straight outwards from their sterigmata. In order to determine the trajectory of a spore I therefore proceeded indirectly. The maximum horizontal distance of propulsion and the terminal rate of fall of a spore in still air were first measured, and then the data so obtained were introduced into an equation based on Stokes' Law. By means of a series of calculations made with this equation the required trajectory was then plotted out.[2] This trajectory,

[1] For a discussion of the form and function of the typical ascus *vide* vol. i, pp. 240–247.

[2] Vol. i, 1909, pp. 184–189, Figs. 64–66.

which I called a *sporabola*, is remarkable in that roughly it can be divided into two parts—a part due to the projection of the spore and a part due to the fall of the spore towards the ground. A spore, shot out horizontally from a gill, goes forward for about 0·1 mm. and then makes a sharp turn through a right angle, after which it falls under gravity vertically downwards with a constant terminal velocity.

To demonstrate the nature of this peculiar trajectory on a large scale, I have invented the *balloon-gun* which has been so named because its projectiles are balloons. In the development of certain guns used in the Great War, the object has been to throw a projectile of large volume and high density a distance of several miles. In developing my balloon-gun, on the other hand, the object has been to throw a projectile of large volume but very small density (*i.e.* just exceeding that of air) a distance of a few feet only. Thus, while the size of my projectiles has not greatly differed from the size of the shells of large field guns, the density has been very much smaller. My projectiles, it must be admitted, although of considerable scientific interest, appear somewhat ridiculous to those who see them in action for the first time, but they have this advantage over the shells of the battlefield: their motions provoke laughter rather than tears.

The balloons which I have used as projectiles have been spherical and oval toy-balloons which, when inflated, resemble in form the two chief types of basidiospores. Their size was varied by choosing larger or smaller envelopes and by altering the amount of gas with which any one balloon was inflated. The spherical balloons were mostly about 6 inches in diameter and the oval ones 10–24 inches long and 6 inches wide. The gas pressed into a balloon was either air or a mixture of air and coal-gas. The mixture, of course, is lighter than air; and, by filling a balloon with a mixture in which the components were suitably balanced, the rate of fall of the balloon could be reduced to whatever was desired. However, most of my experiments were carried out with balloons filled with air.

A toy-balloon which falls very slowly in air resembles a spore in that it has an enormous volume and surface area relatively to its mass. Therefore, not only in having a spherical or oval

shape and a smooth wall but also in its peculiar volume-to-mass and surface-area-to-mass relations, a toy-balloon shows itself particularly well fitted to be used as a large-size model of a basidiospore.

The rate of fall of a spore varies not only with its density but also with its volume and with the amount of its surface exposed to the air, so that, with density constant, the smaller a spore, the slower is its terminal velocity. A variation of the rate of fall with volume can readily be demonstrated to an audience with a balloon. Thus, for instance, it was observed that the same balloon when falling 11 feet in still air took: (1) when uninflated, 1·5 seconds; (2) when partly inflated so that it was 10 inches long and 6 inches wide, 4 seconds; and (3) when fully inflated so that it was 23 inches long and 6 inches wide, 5 seconds. In its three states, in succession, the balloon had about the same weight in air but there was a progressive increase in volume and surface area. The larger the volume of the balloon, the slower was its rate of fall.

Any homogeneous elongated body falling in still air tends to orientate itself in such a way as to present the maximum amount of surface in the direction of the line of fall and thus to fall as slowly as possible. In accordance with this law a piece of paper 4 cm. long and 0·5 cm. wide, when falling, does not approach the earth with an end-wise movement but rather keeps its long axis directed transversely to its line of fall. For certain reasons which will not be discussed here, the piece of paper usually rotates rapidly about its long axis during its descent. An elongated cylindrical object, such as a piece of cotton fibre, hair, or spider's web, when falling (as may be seen in a beam of sunlight), also keeps its long axis parallel with the earth's surface but, unlike the flat piece of paper, does not rotate about its axis. Still smaller cylindrical bodies, such as the spores of *Claviceps purpurea*, doubtless fall like bits of cotton fibre; but even oval spores, which are only two or three times as long as they are wide, also tend to fall with their long axes held horizontally. This I directly observed with a horizontal microscope for the spores of *Polyporus squamosus*, which are three times as long as they are wide.[1] Now this mode of falling of elongated

[1] Vol. i, 1909, pp. 185–189, Figs. 64–66.

spores can be beautifully illustrated with an elongated balloon as follows. A balloon which is 24 inches long and 6 inches wide and having a density just exceeding that of air, is taken in the hand and held with its long axis perpendicular ; and it is then allowed to fall from rest. Almost immediately after its liberation, it turns

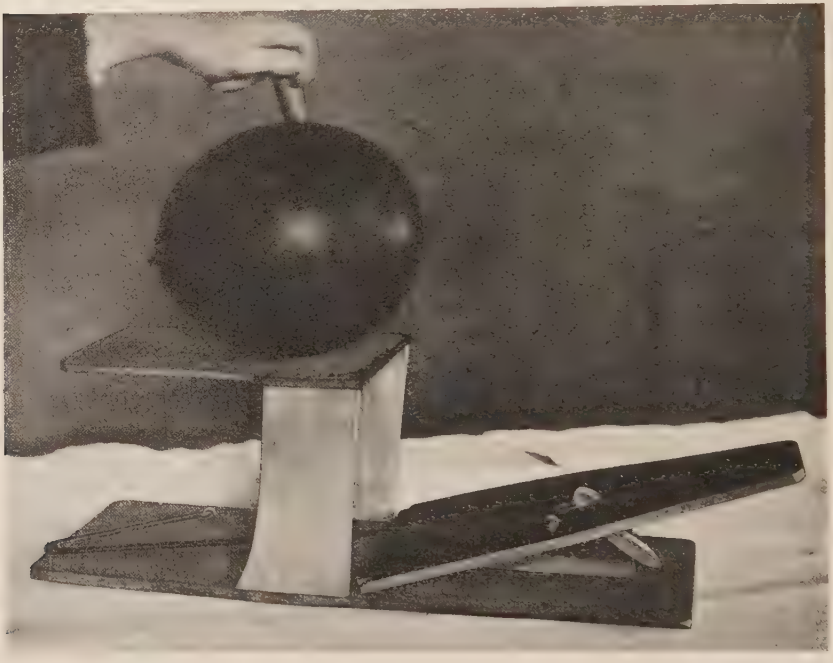


FIG. 13. –The balloon-gun for discharging balloons. A balloon is shown held in position on the platform just before the slamming-board is released by pulling the trigger. The base-board was 2 feet long.

through a right angle and comes to place its long axis horizontally ; and so directed the long axis remains until the balloon has reached the ground. Such an elongated balloon, however liberated, always quickly turns, just as does an elongated spore, until its long axis comes into a horizontal position.

When projected horizontally, toy-balloons filled with air or a mixture of air and coal-gas have a trajectory exactly resembling that which I have described for spores.[1] The simplest way of

[1] Vol. i, 1909, pp. 185–189. Figs. 64–66.

projecting a balloon horizontally forward through the air is to use one's hands for the purpose. A spherical balloon 6 inches in diameter cast by hand as hard as possible in a horizontal direction travels rapidly forward for about 2 or 3 feet and then makes a sudden sharp turn downwards, after which it falls with a slow and even terminal velocity vertically downwards toward the earth. The resistance of the air reduces the horizontal projection-velocity of the balloon to zero in less than a second and, by the end of this time, the balloon has ceased to be carried forward and is simply falling under the influence of gravity. Thus the sporabolic trajectory, which for a spore has a horizontal component only 0·1–0·2 mm. long, can be demonstrated on a large scale to an audience of considerable size.

The balloon-gun which I invented to save myself the trouble of projecting the balloons forward with my hands was of very simple construction (Fig. 13). It was made of wood and consisted of the following parts : (1) a *base-board* 20 inches long and 8 inches wide, (2) two straight upright *arms*, 8 inches high, (3) a *platform* for the projectile, attached to the two arms, (4) a *slamming-board*, 15 inches long and 8 inches wide at its base, hinged below to the base-board along a median transverse line, movable about its hinges through nearly a right angle, *i.e.* from the nearly horizontal position shown in Fig. 13 to a vertical position, in the latter position projecting 7 inches above the top of the platform, (5) a strong *spring* attached to the middle of the slamming-board and to the base-board, and tending to bring the slamming-board into a vertical position, (6) a triangular *trigger-board* attached to the base-board, and (7) a *trigger* attached to the trigger-board, passing upwards through a slot in the centre of the slamming-board, and provided above with a catch. In Fig. 13 the catch of the trigger is holding the slamming-board down.

The balloon to be used as a projectile was set on the top of the platform with one side projecting toward the slamming-board ; and it was held in position very lightly by pressure above applied with a finger. The gun was then fired by pulling the trigger. The movement of the trigger released the catch, whereupon the slamming-board was caused by the spring to swing sharply through

nearly a right angle into a vertical position where further movement was stopped by the arms and platform. The slamming-board, which was 7 inches longer than the platform was high, was thus caused to strike the projecting part of the balloon with considerable violence. In response to the blow from the slamming-board, the balloon shot forward into the air through a horizontal distance of about 3 to 6 feet; and it then made a sharp turn downwards, thus completing its sporabolic trajectory.

The gun was used to discharge both spherical and oval balloons in a horizontal direction, and the results obtained with it did not differ in any essential from the results obtained by casting the balloons forward with the hand. The balloon shown in Fig. 13 was 10 inches long and slightly oval. When fired from the platform, it shot forward to a distance of 6 feet before beginning to fall vertically.

When an elongated balloon, 13 inches long and 6 inches wide, was set on the discharging platform with its long axis in the direction of the axis of the gun and of the line of flight and was then discharged, it was observed that, during its flight, the balloon turned through an angle of 90° so that its long axis, while remaining horizontal, came to be turned in a direction which was transverse to the line of flight. The same result was obtained by casting elongated balloons forward by hand. This turning movement is exactly what one should expect on the principle that a moving body tends to present its greatest surface to the resistance of the air. Theory and observation both permit one, therefore, to draw the conclusion that an elongated spore, when shot from a sterigma or out of an ascus and whilst moving against the resistance of the air, must tend to turn its long axis from its original direction through a right angle.

A Comparison of the Rates of Fall of Spores and Thistle-down. —If the spores of Hymenomycetes, when suspended in the air on an autumn day, were to have their diameters suddenly increased 100 times without this increase altering their normal rate of fall, we should see them with the naked eye, and they would often darken the air and astonish us with their vast numbers and extraordinary variety. We should be most struck, perhaps, by the slowness of their rate of fall. In particular, it would be necessary

for us to watch the smallest spores very carefully indeed if we wished to make sure that they were actually falling.

Every one has noted with delight the very slow rate of fall of thistle-down when being driven before the wind. Yet thistle-down falls very rapidly relatively to the spores of the Hymenomycetes. This fact I have proved by direct comparison of the rates of fall of thistle-down and spores in still air.

Cnicus arvensis, which in Canada is called the *Canada Thistle* although it was introduced from Europe, is as common a weed in Manitoba as in England. I brought some capitula of this species, which bore ripe but not yet fully expanded fruits, into the laboratory at Winnipeg and allowed them to dry. Soon, each fruit opened its parachute-like pappus and some of the fruits became detached from their discs. I took four of these detached fruits and measured their rates of fall in still air through a distance of 6·9 feet. Many measurements were made and it was found that the fruits fell 6·9 feet in 11–12 seconds. The average rate of fall was 6·6 inches or 167·6 mm. per second.

The rates of fall of the spores of various species of Hymenomycetes were measured, as described in Volume I, with a horizontal microscope and a drum recorder.[1] The large spores of *Amanitopsis vaginata* fall in moderately dry air at the rate of 4·29 mm. per second, the medium-sized spores of the Wild Mushroom (*Psalliota campestris*) and of *Polyporus squamosus* at 1·61 mm. per second and 1·03 mm. per second respectively, and the small spores of *Collybia dryophila* at 0·49 mm. per second. These rates of fall along with the rate of fall of the fruits of *Cnicus arvensis* may be set out in tabular form as follows :

Rates of Fall in Still Air of Thistle Fruits and of the Spores of Hymenomycetes

Cnicus arvensis	167·6	mm. per second
Amanitopsis vaginata	4·29	,, ,,
Psalliota campestris	1·61	,, ,,
Polyporus squamosus	1·03	,, ,,
Collybia dryophila	0·49	,, ,,

[1] Vol. i, 1909, pp. 166–177.

From these data a simple calculation shows that the Thistle fruits fall with a steady terminal velocity which is :

39 times that of the spores of Amanitopsis vaginata,
104 ,, ,, ,, ,, the Wild Mushroom,
162 ,, ,, ,, ,, Polyporus squamosus, and
342 ,, ,, ,, ,, Collybia dryophila.

These figures serve to indicate how very much more slowly the spores of Hymenomycetes fall than the parachute-like fruits of a typical Thistle. On a windy day, one often sees thistle-down blowing for very long distances over hills and plains ; but, on such a day, the invisible spores of the Hymenomycetes which, as we have seen, fall so very much more slowly than thistle-down, must be transported by the wind with even much greater ease than this delicate material and must, therefore, often be carried for many miles before they finally come to earth.

A Comparison of the Rates of Fall of Spores and Bacteria.—In still air, the spores of the Hymenomycetes fall much more slowly than thistle-down or the winged seeds and fruits of Flowering Plants but, nevertheless, they fall very much faster than Bacteria. Among organic bodies adapted for passive dispersal by the wind, they therefore occupy only an intermediate position.

Spherical species of Bacteria—Micrococci, Streptococci, etc.—are much smaller than the spores of the Hymenomycetes. Their diameters vary from about 2 to $0{\cdot}2\,\mu$. The rate of fall of individual bacteria may be calculated by using the second equation given on p. 21. Now, for our purposes, ρ may be taken as 1, σ as negligibly small, μ as $1{\cdot}8 \times 10^{-4}$, g as 1000, and p as 76 cm. of mercury. The following Table gives the diameter, radius, terminal velocity of fall in still air, and time required to fall $2{\cdot}5$ cm. (approx. 1 inch) for the individual cells of certain species of spherical bacteria.

The cells of the largest species, *Micrococcus Freudenreichii*, which have a diameter of $2\ \mu$ and a radius of $1\ \mu$, fall only about one-eighth of a millimetre in a second and, to fall $2{\cdot}5$ cm. or 1 inch, require 3 minutes and 8 seconds.

The cells of the smallest species, *Streptococcus gracilis*, which have a diameter of $0{\cdot}2\ \mu$ and a radius of $0{\cdot}1\ \mu$, fall only about

one five-hundredth part of a millimetre in a second and, to fall 2·5 cm. or 1 inch, require 3 hours and 5 minutes.

The ideas of most people concerning the speed of falling bodies are gained by observing the fall of comparatively large objects, and it is therefore a little difficult to realise that there are living organisms which, when falling in still air, require upwards of three

Rates of Fall of Spherical Bacteria in Still Air.

Species.	Diameter in μ.	Radius in μ.	Terminal Velocity in mm. per sec.	Time taken to Fall 2·5 cm. or 1 inch.
Micrococcus Freudenreichii .	2·0	1·0	0·133	3 mins. 8 secs.
Micrococcus bicolor . .	1·2–1·6	0·7	0·0675	6 mins. 10 secs.
Micrococcus luteus . .	1·2–0·4	0·4		
Micrococcus roseus . .	1·0–0·6	0·4	0·0237	17 mins. 30 secs.
Micrococcus pyogenes aureus .	0·8	0·4		
Micrococcus cerasinus . .	0·3	0·15	0·00428	1 hour 37 mins.
Streptococcus gracilis [1] . .	0·2	0·1	0·00224	3 hours 5 mins.

hours to fall a single inch ; but such an organism is *Streptococcus gracilis*. The individual cells of this bacterium, under natural conditions, probably fall even more slowly than our calculation has shown owing to the fact that, when isolated in the air, they would be dried up and therefore have a smaller diameter than 0·2 μ which was measured when they were immersed in a culture medium.

The rates of fall per second and the length of time required to fall an inch for (1) thistle-down, (2) moist basidiospores,[2] and (3) bacteria may be tabulated as shown in the Table on page 42.

From a comparison of the data given in the Table it is evident that the rates of fall of basidiospores are intermediate between the rates of fall of Thistle fruits and of the cells of bacteria. Thus the rate of fall of a Thistle fruit is about one hundred times that of a Mushroom spore, but the rate of fall of a Mushroom spore is about twelve times that of the cells of *Micrococcus Freudenreichii* and about seven hundred times that of the cells of *Streptococcus gracilis*.

The minute size of wind-disseminated cells, whether they be

[1] The velocity of fall here given for *Streptococcus gracilis* is 82 per cent. greater than that given by the uncorrected equation for Stokes' Law (first equation on p. 21), while that for *Micrococcus Freudenreichii* is only 8·2 per cent. greater.

[2] Vol. i, 1909, p. 175.

basidiospores, mould spores, yeast cells, bacteria, or pollen grains, is advantageous to the species concerned in at least two ways: (1) it permits of these cells being produced in vast numbers so that the chances that some of them will settle in favourable positions is greatly increased and (2), being correlated with a very slow rate of fall, it enables the wind to carry the cells relatively very long distances before they settle, thus assisting the agent of dispersal.

In concluding this section, it may be pointed out that a spore or

Comparative Rates of Fall of Thistle-down, Basidiospores, and Bacteria in Still Air.

Objects Falling in Still Air.	Rate of Fall in mm. per second.	Time taken to Fall 2·5 cm. or 1 inch.
A fruit of Cnicus arvensis . .	167·6	0·15 second
A spore of Amanitopsis vaginata .	4·29	5·8 seconds
A spore of a Wild Mushroom . .	1·61	15·5 seconds
A spore of Polyporus squamosus .	1·03	24·3 seconds
A spore of Collybia dryophila . .	0·49	51·0 seconds
A cell of Micrococcus Freudenreichii	0·133	3 minutes 8 seconds
A cell of Streptococcus gracilis .	0·00224	3 hours 5 minutes

bacterium, on being cast into the air, must, unless the air is absolutely saturated with water vapour, dry up immediately. The rapidity with which basidiospores dry up when they fall from the hymenium of an agaric on to a slide placed beneath them in a laboratory, is well known, and I have remarked upon it in Volume I.[1] In ordinary unsaturated air, either in the laboratory or in the open, the spores of Hymenomycetes dry up in a few seconds. Doubtless, under similar conditions, Micrococci and Streptococci dry up in less than one-tenth of a second. A spore or bacterium, therefore, when floating in the air, must be thought of as existing in a condition not of turgidity but of desiccation.

[1] Vol. i, 1909, p. 162.

CHAPTER II

THE RATE OF DEVELOPMENT OF INDIVIDUAL SPORES IN DIFFERENT SPECIES

Introduction and Table of Results—Methods—Discussion of Results—Effect of Temperature

Introduction and Table of Results.—In order to increase the exact data concerning the production and liberation of spores in the Hymenomycetes, it seemed to me advisable to measure the interval of time which elapses between the first appearance of a spore on the end of the sterigma as a tiny rudiment and the moment of spore-discharge. The first observations of this nature were made upon *Calocera cornea* and have already been recorded in the previous Chapter. Subsequently, the investigation was extended to a number of other species with spores differing from one another in size, shape, colour, and thickness of cell-wall. The results obtained have been embodied in the adjoining Table. The time given in the fourth column is the average time taken for the development and discharge of the first of the four spores to be shot away from each basidium. The number of basidia upon which observations were made was usually from three to six.

Methods.—The method generally employed for observing spore-development in the Agaricineae was as follows. A tiny drop of water was placed on the middle of the base of a compressor cell (Fig. 14) and spread out. The whole of a small gill or a large fraction of a large gill was then dissected from a freshly-gathered vigorously-growing fruit-body and laid over the drop, so that the water partly or wholly filled the space between the gill and the glass. Then another small drop was placed on another part of the compressor-cell base. Finally, the cell was closed by its glass cover which was pressed down a little way. The upper side of the

gill thus came to be exposed to moist air, without being wetted by free water or receiving mechanical interference from the compressor-cell cover. Usually the hymenium was observed with the low power of the microscope (Zeiss : objective AA, eye-piece 4, tube drawn out full, magnification about 130) ; but, sometimes, when the lid of the compressor cell had been pressed down so that it was in contact with part of the upper surface of the gill, it was

Average Time taken for the Development and Ripening of an Individual Spore from the Moment the Spore appears on the Sterigma as a Tiny Rudiment until the Moment of Discharge.

		Species.	Hrs.	Mins.	Spore-colour.	Spore-wall.
Fruit-bodies.	Can be revived after desiccation.	Collybia velutipes	0	47	colourless	smooth
		Dacryomyces deliquescens	0	50	,,	,,
		Collybia fusipes	1	3	,,	,,
		Marasmius oreades	1	5	..	..
		Exidia albida	1	15	..	..
		Calocera cornea	1	20	..	..
	Cannot be revived after desiccation.	Armillaria mellea	1	30	..	..
		Collybia radicata	1	30	,,	..
		Pluteus cervinus	3	25	pink	,,
		Nolanea pascua	4	15	pink	polyhedral
		Russula cyanoxantha	5	10	colourless	warted
		Stropharia semiglobata	5	40	purple-brown	smooth
		Panaeolus campanulatus	7	30	black	,,
		Psalliota campestris (cultivated)	8	0	purple-brown	,,
		Coprinus sterquilinus	32	0	black	,,

found possible to use the high power (objective DD, eye-piece 4, tube in, magnification about 440).

The chief difficulty in the application of the method consists in supplying enough yet not too much water to the gill, but experience soon teaches one how to overcome it. Sometimes the gill was laid on the compressor cell without any water being first placed below it. In that case a very little water was touched to the edge of the gill which had once joined on to the flesh. For *Hygrophorus ceraceus* and *Bolbitius flavidus* observations showed that it was best not to wet the gills at all. Each case, in the matter of water supply, requires to be considered individually.

Not infrequently the cover-glass of the compressor cell became

fogged just above the gill, owing to condensation of water vapour upon it. In order to clear the fog away, it was necessary to remove the top of the cell for a few seconds until the condensed moisture had evaporated or to leave the cover-glass in position and to warm it gently from above with a finger or heated needle. To avoid fogging altogether or reduce it to a minimum, it was found advisable to use diffused daylight reflected with the plane mirror and to have the cover-glass well raised above the gill under observation.

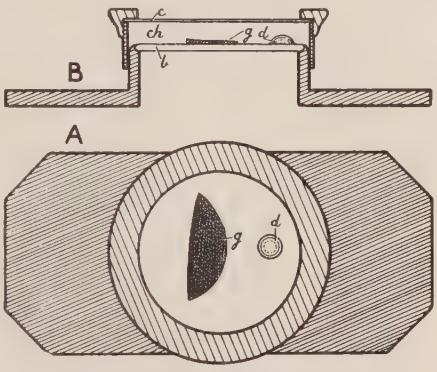


FIG. 14.—A compressor cell used for observing the development and discharge of spores on the hymenium of Hymenomycetes. A, viewed from above; *g*, a gill of an Agaric; *d*, a water-drop. B, vertical section; *b*, the glass base of the cell; *c*, the cover-glass; *ch*, the moist chamber; *g*, a gill; *d*, a water-drop. The frame-work of the cell was made of brass. The chamber, *ch*, can be made larger or smaller by raising or lowering the cap of the cell. Actual size.

For *Collybia velutipes* (Fig. 15), where the time of observation was only three-quarters of an hour, the gill was rested on a drop of water on an ordinary slide. Owing to the weather conditions being very damp and the air in consequence being almost saturated with water vapour, it was not even necessary to cover the gill with a cover-glass: the spores developed quite normally when the hymenium was directly exposed to the high objective. For *Marasmius oreades* a similar preparation was made with the exception that a cover-glass was laid over the gill. Here again, the development of the spores was very rapid (just over an hour), and the air was very moist. Where, however, as in *Stropharia semiglobata*, spore-development takes some hours, the compressor cell is indispensable for keeping the gill continuously moist.

The observations on *Panaeolus campanulatus* were made with a horizontal microscope under conditions which will be described in Chapter X.[1] For *Coprinus sterquilinus* individual spores were

[1] Chapter X, section: "Apparatus and Method for Observing the Development of the Hymenium."

not observed for 36 hours, but the length of time required for their development was estimated by a sufficiently reliable comparative method, the nature of which will be explained in Volume III in connection with a discussion of the development of the hymenium.[1]

Where a gill was comparatively thin and translucent (*Stropharia semiglobata*, *Collybia velutipes*, etc.), just sufficient light passed through its whole substance to permit of spore-development being observed anywhere on the hymenium covering the upper side of the gill. However, to watch the four spores on a particular basidium projecting upwards to the eye, from their first origin to their discharge, by a dim light, and for several hours with but short occasional breaks, is somewhat tedious work and rather trying for the eyes ; and one may be pardoned perhaps, if, when one's vigil of watchful waiting has at length been brought to a successful close by the dramatic shooting off of the four microscopic projectiles, one's pleasure is mixed with a feeling of relief. When a gill was comparatively thick and but feebly translucent (*Marasmius oreades*, *Collybia radicata*, *Hygrophorus ceraceus*, etc.), it became necessary to turn one's attention to the basidia projecting freely from that edge of the gill which normally looks down toward the earth. Under these conditions the basidia and spores were observed in lateral view.

The fruit-bodies of *Exidia albida* and of *Dacryomyces deliquescens* were cut in half ; one half was laid with its plane of section more or less in contact with the base of the compressor cell ; a drop of water was added ; the compressor cell was closed ; and then the basidia and spores were observed in lateral view with the low power of the microscope.

The question arises whether or not the gills or parts of fruit-bodies placed in the compressor cell continued to develop their hymenium normally. In my opinion the answer, for all the species named in the Table, must be in the affirmative. By experience, one becomes used to normal spore-development, which is characterised by great regularity in the rate of increase in size and, where the spore-walls become pigmented, in the rate of pigmentation, and also characterised by the excretion of a drop of water of a

[1] Vol. iii, Chap. III, section : "The Structure and Development of the Hymenium."

definite size from the hilum of each spore just before discharge.

FIG. 15.—*Collybia velutipes*, a species with thin, smooth, colourless spore-walls, which develops its individual spores very rapidly: the interval elapsing between the first formation of a spore on its sterigma as a tiny rudiment and its discharge is less than 1 hour (about 47 minutes). The fungus has a brown velvety stipe and is often found in autumn on dead trunks of trees and about stumps in Europe and North America. Photographed at Scarborough, England, by A. E. Peck. Natural size.

Normally, too, the time from the origin to the discharge of a spore is very constant under the same conditions for each species: its

range of variation is usually within 10 per cent. of the mean time, on each side of the mean. If development is abnormal, this constancy is changed for considerable irregularity : the rate of spore-growth may become much slower than is normal ; all growth may entirely cease ; half-grown or full-sized spores may bend toward one another, touch, and form with the sterigmata a single mass which collapses and sinks downwards on to the basidium-body below ; drops of excessive size may be excreted from the hila of quite immature spores ; and apparently mature spores, with or without the excretion of drops, may not be discharged at all. Owing to abnormalities of the kind indicated, I was unable to make complete observations of the period of spore-development in the following species : *Hygrophorus conicus*, *H. ceraceus*, *Corticium Solani* (*Rhizoctonia Solani*), and *Bolbitius flavidus*. Drops of water were not excreted at the hila of the spores at the time they should have been : instead, the basidia collapsed and dragged the spores with them on to the hymenium. Lack of leisure prevented me from making further attempts to observe the completely normal spore-development in these species.

Discussion of Results.—We may now turn to the results of the observations. A glance at the Table shows that there are great differences in the length of time the spores remain on the sterigmata in different species. Thus, in *Collybia velutipes*, the time is only 47 minutes, whereas in *Panaeolus campanulatus* it is about 7 hours and 30 minutes, *i.e.* more than nine times as long. In *Coprinus sterquilinus* the time is about 32 hours, *i.e.* nearly forty times as long as in the Collybia and nearly four times as long as in the Panaeolus. It is only to be expected that these very diverse rates of spore-development should be correlated with other fruit-body characters. A discussion of these correlations will now follow.

Mere size is no guide to the rate of spore-development, and one cannot say : the larger the spore, the longer it takes to develop. The small spores of some species actually develop more slowly than the larger spores of other species. Thus the spores of the cultivated Mushroom, *Psalliota campestris*, which measured $7 \cdot 25 \times 5 \cdot 6\ \mu$ took only about 8 hours to develop from their first origin to discharge, whereas the larger spores of the Fairy Ring Fungus, *Marasmius*

oreades, which measured $9{\cdot}5 \times 5{\cdot}6$ μ took 1 hour and 5 minutes.

So long as a spore has a smooth, rounded wall, the rate of development does not seem to be specially influenced by spore-shape and is not correlated with greater or less rotundity. As we shall see shortly, however, the rate may be affected by the flattening of the cell-wall so as to give the spore a polyhedral form, and by the development of warts.

Collybia velutipes, *Dacryomyces deliquescens*, *Marasmius oreades*, *Exidia albida*, and *Calocera cornea* all have very short periods for their development, namely, from 47 minutes to 1 hour and 20 minutes. The period for *Collybia dryophila* was also found to be a little more than one hour, but it was not measured exactly and therefore has not been included in the results given in the Table. All these species are characterised by the fact that they can withstand desiccation for some days or weeks without any impairment of their vitality: when the dried fruit-bodies are moistened once more, they completely revive and within a very few hours begin to liberate a fresh crop of spores.[1] All these species have spores with smooth, thin, colourless walls. It would appear that their fruit-bodies are so organised that they can make the best use of temporary moist weather-conditions by beginning to discharge spores as soon as possible after they have been re-wetted by rain water. *Collybia fusipes*, which can develop and shed its spores in just over one hour, has been set down in the Table as having fruit-bodies which can withstand desiccation. This, however, is so far only a supposition; it is not the result of experiment and may not be true. All that has been ascertained at present is that the young fruit-bodies can lose a considerable amount of water without injury and that, like *Marasmius oreades*, etc., they can reabsorb water when this is brought into contact with their pilei.

Armillaria mellea and *Collybia radicata*, species which grow on wood and have smooth, thin-walled, colourless spores, also develop their spores very rapidly—in 1 hour and 30 minutes. Possibly this rapid rate of development is associated with the fact that both species grow on wood and are therefore subject to the danger

[1] *Vide* these *Researches*, vol. i, 1909, Chap. IX, pp. 105–119.

of receiving too little water for their development. *Lepiota procera* is a typical white-spored species growing on the ground; but it has thick walls to its spores. In this fungus I found that the time taken for spore-development was more than two hours; but, owing to an unavoidable interruption, I was unable to complete the investigation. Another terrestrial white-spored species examined was *Hygrophorus ceraceus*. Unfortunately, although its spores apparently grew to maturity in a normal manner, their discharge was not effected: they were dragged down on to the hymenium by their basidia when these collapsed. However, I have little doubt, from the observations made, that the period of spore-development up to the moment of discharge in this species is about 3 hours and 30 minutes. *Hygrophorus conicus* was also found to develop its spores very slowly, and I suspect that the Hygrophori, all of which are characterised by possessing fruit-bodies with an extraordinarily waxy consistence, develop spores more slowly than the species of Collybia, Marasmius, and Armillaria.

Proceeding down the list given in the Table we find that from *Pluteus cervinus* onwards the time taken for spore-development is relatively long. All these remaining species have spores which either are coloured or are provided with irregular walls. *Pluteus cervinus* and *Nolanea pascua* both have pink spores and take 3 hours 20 minutes and 4 hours 15 minutes respectively to develop their spores. In the former species the spore-walls are smooth whereas in the latter they are more complex, for they become polyhedral. Perhaps this added complexity in the Nolanea accounts for the fact that this species takes about an hour longer than the Pluteus to develop its spores.

Russula cyanoxantha has spores which are colourless but possess warted walls. Here again, the warting of the walls seems to be a factor increasing the time required for spore-development, which in this case amounts to 5 hours and 10 minutes.

The remaining species in the Table have highly pigmented spore-walls. *Stropharia semiglobata*, with brown-purple spores, takes 5 hours and 40 minutes for spore-development. *Psalliota campestris* (the cultivated form), also with brown-purple spores, was observed to take 8 hours; but, possibly, with fresher material than

I had at my disposal, this period might be somewhat shortened. *Pholiota praecox*, a species with brown spores, was found in an uncompleted investigation to take upwards of 6 hours. *Panaeolus campanulatus*, with black spores, has a period of about 7 hours and 30 minutes. For *Anellaria separata* (Fig. 16), which also has black spores, where observations were made in the same manner as for *Panaeolus campanulatus*, *i.e.* with the horizontal microscope, the period was observed to be between 9 and 10 hours. For *Coprinus sterquilinus*, which has very black spores, the period of spore-development was found to be the longest of all, namely, 32 hours. For *Bolbitius flavidus*, which has spores with bright yellow walls, the period is also a very lengthy one, roughly 8 hours; but in this case the final phase of discharge was not satisfactorily observed. If we compare the seven markedly chromosporous species which have just been named with the leucosporous and rhodosporous species already considered, it would appear that the high pigmentation of the spore-walls is associated with a prolonged period of spore-development. We are justified in thinking of such genera as Marasmius, Collybia, and Armillaria as

FIG. 16.—*Anellaria separata*, a species with thick black spore-walls, which develops its individual spores very slowly: the interval elapsing between the first formation of a spore on its sterigma as a tiny rudiment and its discharge is from nine to ten hours. The fruit-bodies are coming up on dung covered by herbage. On the extreme left is a fruit-body of *Coprinus niveus* in the last stage of autodigestion. This species also has black thick-walled spores which develop relatively slowly. Photographed by A. E. Peck at Scarborough, England. About $\frac{1}{2}$ natural size.

rapid producers of individual spores, and of such genera as Panaeolus, Stropharia, and Coprinus as slow producers of individual spores.

Fayod, who was an excellent observer, asserts in his *Prodrome* that the Leucosporae, with few exceptions, have simple spore-walls; whilst, in the majority of the Agaricineae with pigmented spores, the spore-walls are double. He further asserts that, where a spore is coloured and two-coated, it is the endospore and not the exospore which contains the pigment.[1] I have not as yet sought to verify these statements in a detailed investigation; but it may be remarked that I have only been able to observe a single wall-layer in the spores of species of Marasmius, Collybia, and Armillaria, whereas in the large spores of *Coprinus sterquilinus* when mounted in water I have clearly perceived, on the side of the spore opposite to the hilum, an outer white membrane surrounding an inner membrane containing the dark pigment. Moreover, I have confirmed Hansen's [2] statement that, when the spores of *Coprinus stercorarius* are treated with chlor-zinc iodine, an outer colourless cell-wall or exospore swells up and removes itself from an inner pigmented cell-wall or endospore.[3] If we assume Fayod's statements to be correct, we may consider that, in general, pigmented spores take longer to develop than colourless ones, not merely because they have to manufacture a pigment but because they have to form an inner wall which comes to contain that pigment.

Another factor which is probably correlated with the slower development of highly pigmented spores is that, where these spores are concerned, as compared with colourless spores, there is a relatively greater crowding of basidia producing spores simultaneously on a unit area of the hymenium. The contrast in this respect between,

[1] M. V. Fayod, "Prodrome d'une Histoire Naturelle des Agaricinés," *Ann. sci. nat.*, T. IX, 1889, pp. 269, 302, and 330.

[2] E. C. Hansen, "Biologische Untersuchungen über Mist-bewohnende Pilze," *Bot. Zeit.*, 1897, p. 114.

[3] In some Ascomycetes having pigmented spores, the spore-wall consists of two layers as in *Coprinus stercorarius*. Thus a double spore-wall is present in *Daldinia vernicosa* and *D. concentrica*; for A. S. Rhoads ("*Daldinia concentrica*—a pyroxylophilous Fungus," *Mycologia*, vol. x, 1918, p. 283) has pointed out that, when the spores of these species are mounted in dilute alkaline solutions, the colourless exospore dehisces along a single equatorial line and thus separates in two pieces from the black endospore.

on the one hand, species of the genera Psalliota, Stropharia, Panaeolus, and Coprinus, and, on the other hand, species of Collybia, Marasmius, Armillaria, Russula, and Hygrophorus, is marked. Illustrations of this difference will be given subsequently in this and the next volume.

In *Lepiota procera*, the well-known Parasol Fungus, the spore-bearing basidia are just as crowded as in a Panaeolus. Moreover, the spores have thick walls. Fayod,[1] in an illustration, has clearly shown the thick inner endospore lying inside the exospore. This fungus is therefore exceptional in the Leucosporae. I suspect that the time required for development of its individual spores will be found to be much longer than in most Leucosporae, such as species of Collybia, Marasmius, etc.

The very long period of time required for the development of individual spores of *Coprinus sterquilinus*, namely, 32 hours, calls for some special remarks. As will be made clear in a subsequent Chapter, there are two main types of fruit-body mechanism for the production and liberation of spores : the non-Coprinus type and the Coprinus type. In the former, on any small area of the hymenium (*e.g.* 1 square mm.) there is a series of successive generations of basidia which bring their spores to maturity in succession ; so that, although spore-production for an individual basidium takes but a short time—not more than a few hours—yet spore-production is continued for several days. In the latter, on the other hand, on any small area of the hymenium, all the basidia produce their spores practically simultaneously and the basidia are extremely crowded owing to the occurrence of dimorphism. The very slow rate of development of individual spores in *Coprinus sterquilinus* seems to me to be correlated with the simultaneous development of the spores and the extreme crowding of the basidia. Doubtless, in many of the smaller Coprini, the rate of spore-development is much less than 36 hours ; but I have reason to suspect that a very slow rate characterises the whole genus. *Coprinus sterquilinus* has very large spores, 20 × 11 μ, the largest which I have met with during the examination of nearly thirty species of Coprinus. It may therefore be

[1] M. V. Fayod, *loc. cit.*, Pl. 6, Fig. 9.

that the extraordinarily long period for spore-development in this species is to some extent due to the very large size of the spores.

The time taken for the development of a single spore may be divided into two parts: (1) the time employed by the spore in growing to full size, and (2) the time employed in the subsequent process of ripening, which is terminated by spore-discharge. These times are given for a few species in the following Table.

The Development of Individual Spores.

Species.	Time required for				Total Time.	
	Growth to Full Size.		Ripening.			
	Hrs.	Mins.	Hrs.	Mins.	Hrs.	Mins.
Collybia velutipes	0	15	0	32	0	47
Collybia fusipes	0	20	0	43	1	3
Collybia dryophila	0	20	0	? 50	? 1	10
Armillaria mellea	0	20	1	10	1	30
Dacryomyces deliquescens	0	23	0	27	0	50
Marasmius oreades	0	35	0	30	1	5
Collybia radicata	0	35	0	55	1	30
Calocera cornea	0	40	0	40	1	20
Psalliota campestris (cultivated)	0	40	7	20	8	0
			more than		more than	
Pholiota praecox	0	45	5	20	6	0
Hygrophorus ceraceus	1	0	? 2	30	? 3	30
Stropharia semiglobata	1	10	4	30	5	40
Russula cyanoxantha	1	45	3	25	5	10
Nolanea pascua	2	30	1	45	4	15
	about		about		about	
Coprinus sterquilinus	9	0	23	0	32	0

From the above data one may conclude that spores usually take longer to ripen than they do to grow to full size from a tiny rudiment; but to this rule *Nolanea pascua*, which has curious polyhedral spores, is an exception. We may further conclude that the length of time taken to grow to full size is no indication of the length of time required for the ripening processes. This is shown by the fact that the spores of *Collybia fusipes*, *Collybia dryophila*, and *Armillaria mellea* all take 20 minutes to grow to full size, yet

after attaining full size they remain on the sterigmata for periods varying from 43 minutes in the first species to 1 hour and 10 minutes in the third. Furthermore, the spores of *Calocera cornea* and of *Psalliota campestris* both take 40 minutes to develop to full size; yet those of the former take only 40 further minutes for their ripening processes whereas those of the latter require more than 7 hours. It is to be noticed for the species investigated, however, that the spores which grow to full size in the least time, namely, those of *Collybia velutipes*, ripen in the fastest time, while those which grow to full size in the maximum time, namely, those of *Coprinus sterquilinus*, take the longest time for ripening. Among the Leucosporae, it is to be noted that the spores of *Russula cyanoxantha*, which are warted, take much longer to grow to full size than any of the smooth-walled spores.

The ripening of a spore involves a good many processes, among which one may perceive the following: (1) the transference of protoplasm from the basidium-body through the sterigma into the spore-lumen, a process which continues long after a spore has attained full size and which leads to the emptying of the basidium-body; (2) frequently, the division of the nucleus which has entered the spore through the sterigma; (3) chemical changes, such as the conversion of glycogen into non-glycogenous products (observed in *Coprinus sterquilinus*); (4) the frequent formation of a thick, pigmented inner wall or endospore; and (5) a preparation for spore-discharge by some alteration at the hilum, of which the excretion of a drop at the hilum a few seconds before spore-discharge is a very obvious sign. It is not surprising that all these changes should take a good many minutes or even hours for their accomplishment.

Already, in a section of Chapter I, a detailed account was given of the development and discharge of the spores of *Calocera cornea*. It will be of interest in this place to give some corresponding details for *Stropharia semiglobata* which, unlike the Calocera, has highly pigmented spores. The time scale in the following Table will be regarded as starting at zero. The mean times given were obtained by observing the development of the spores on six different basidia.

Development of Individual Spores of Stropharia semiglobata.

Observations.	Hours.	Minutes.
First rudiments of spores appear on the sterigmata	0	0
The spores have attained full size	1	10
The spore-walls begin to be pigmented	2	10
The spore-walls are fully pigmented	4	40
The first spore on each basidium is discharged	5	40
The spores are all discharged	5	50 approx.
New spores begin to develop on adjacent basidia	6	0 approx.

The Table shows that each spore, on the average, took an hour and ten minutes to attain full size and that, after this, the spores remained colourless for an hour. Then the process of pigmentation of the walls began and the spore-walls continued to deepen in colour for two and a half hours. After pigmentation had been completed, the spores remained on their sterigmata for one hour more, at the end of which time one spore on each basidium was discharged. The other three spores on each basidium were discharged within about ten more minutes. After another ten minutes a new set of basidia was observed to be developing a new set of spores, so that at the end of six hours a hymenial picture was presented almost precisely similar to that with which the observations began.

The process of pigmentation of the spore-walls is evidently a long one. In *Stropharia semiglobata*, as we have seen, it takes some two and a half hours. In *Panaeolus campanulatus* it was observed to take fully an hour and a half, and in *Coprinus sterquilinus* several hours.

Effect of Temperature.—The development of a spore is due to processes of growth. Now, since growth in general is dependent on temperature, there can be but little doubt that the spores of agarics develop relatively slowly in cold weather and relatively fast in warm weather. A systematic study of the effect of temperature on spore-development would yield interesting results ; but, unfortunately, up to the present, the writer has not found time to undertake it.

For *Collybia radicata*, evidence that the rate of spore-develop-

ment varies with temperature is provided by the following series of observations. On August 12, 1922, which was a very cold day for the time of the year, with a room temperature of about 58°–60° F., the interval of time elapsing between the first appearance of a spore on its sterigma as a tiny rudiment and its discharge was found, as an average for five basidia, to be 2 hours 26 minutes.[1] The gill was left in the compressor cell overnight. The next day, August 13, was sunny and relatively warm, so that the room temperature was raised to about 70° F. New observations were made and it was found that the interval of time elapsing between the first appearance of a spore on its basidium and its discharge was now only 1 hour and 34 minutes, a reduction of 52 minutes as compared with the previous day.[2] Since the observations on the two successive days were made on the same gill confined within an undisturbed compressor cell, and since the only difference in the conditions was one of temperature, it seems clear from the results obtained that in *Collybia radicata* the individual spores develop much faster at high temperatures than they do at low ones.

[1] Observations spread over eight hours and made conjointly by myself and my nephew, Bernard A. Workman. The basidia were all seen projecting beyond the free edge of the gill. The intervals for the five basidia were: 2 hours 30 mins., 2 hours 25 mins. (measured by myself); 2 hours 22 mins., 2 hours 25 mins., 2 hours 30 mins. (measured by B. A. W.).

[2] The interval of 1 hour 30 mins. given in the first Table in this Chapter was determined for another *Collybia radicata* fruit-body in 1916.

CHAPTER III

VARIOUS OBSERVATIONS

The Suppression of the Gills of *Lactarius piperatus* as a Result of the Attack of *Hypomyces lactifluorum*—Sterile Fruit-bodies—The Monstrous Fruit-bodies of *Polyporus rufescens*—The Grafting of Fruit-bodies—The Dwarf Fruit-bodies of *Coprinus lagopus*—The Cultivation of *Marasmius oreades* for Food

The Suppression of the Gills of Lactarius piperatus as a Result of the Attack of Hypomyces lactifluorum.—About eighteen years ago, when I first began to search for fungi in the neighbourhood of Winnipeg, my attention was attracted to some large, thick-fleshed, infundibuliform fruit-bodies (Figs. 17 and 18) which were remarkable in that they looked as though they should belong to the Agaricaceae, but were nevertheless lacking in gills. The under side of the pileus in these fungi was usually quite smooth (Fig. 17, left-hand fruit-body), and only in some specimens were there what seemed to be traces of gills in the form of slight, obtuse ridges stretching radially from the top of the stipe to the edge of the pileus (Fig. 17, right-hand fruit-body). The under side of the pileus was remarkable not only for the absence of gills but also because of its colour, for, unlike the upper surface which was creamy white, it was brilliant orange.

A closer examination of the smooth under side of the pileus revealed the fact that everywhere in its surface layer were embedded large numbers of bright red perithecia with slightly protruding ostiola. It became evident that the fruit-body had been attacked by a Hypomyces. The parasite was then identified as *Hypomyces lactifluorum* (Schw.) Tulasne, a fungus which is not uncommon in various parts of North America.

McIlvaine [1] states that *Hypomyces lactifluorum* occurs in North

[1] C. McIlvaine and R. K. Macadam, *Toadstools, Mushrooms, Fungi, edible and poisonous; One Thousand American Fungi, etc.*, Indianapolis, U.S.A., 1902, p. 562.

America on Lactarius, especially upon *Lactarius piperatus*. Since first becoming acquainted with the parasitised agaric at Winnipeg, I have found it in considerable numbers at Gimli on Lake Winnipeg, at Kenora on the Lake of the Woods, and at Minaki and White Dog upon the Winnipeg River in Western Ontario. I have frequently observed it in company with *Lactarius piperatus*, and a comparative study of the two fungi in the woods has convinced me that in Central Canada the host plant of the Hypomyces is usually, if not always, *Lactarius piperatus*. My observations on the host-species of the Hypomyces thus confirm those of McIlvaine.[1]

The fruit-bodies of *Lactarius piperatus* are attacked by the Hypomyces before they come above the ground, and it is possible that they are infected when extremely small and young. The time and mode of infection are as yet unsolved phytopathological problems. Although many of the infected Lactarii retain their symmetry of form (Figs. 17 and 18), others exhibit more or less irregularity, their stipes being abnormally thick, and their pilei excentric and contorted.

Lactarius piperatus, when parasitised by the Hypomyces, not only has the development of its gill-system inhibited but also its hymenium, so that is is rendered *perfectly sterile*. It produces *no basidiospores whatsoever* and yet its general vigour seems to be in no way diminished. Its fruit-bodies, although often misshapen, have a massive appearance and its pilei are not infrequently 4–5 inches in diameter, *i.e.* as large as those of the largest unparasitised fruit-bodies. A comparison of parasitised and unparasitised fruit-bodies even gives the impression that the former have the thicker flesh and the greater weight. When a tangential section is cut through the side of the pileus, one sees near the lower even edge a wavy line of tissue which, doubtless, is a trace of

[1] I have never found *Hypomyces lactifluorum* in England or met with any one who has. It is not mentioned by C. B. Plowright in his *Monograph of the British Hypomyces* (Grevillea, vol. xi, 1882). However, at King's Lynn in three successive seasons, Plowright found a yellowish-green Hypomyces, *H. luteo-virens*, which, like *H. lactifluorum*, attacks agarics before they appear above the ground and so alters its hosts that it is difficult or impossible to determine their species. Karsten (*vide* Plowright, *loc. cit.*, p. 1) says that he found *H. luteo-virens* on Lactarii in Finland. Presumably, this fungus, which I have not seen, like *H. lactifluorum*, inhibits the development of the gills of its host.

FIG. 17.—Fruit-bodies of *Lactarius piperatus* attacked by *Hypomyces lactifluorum*. The perithecia are thickly dotted over the under side of the pileus. In the right-hand fruit-body the gills are reduced to ridges; in the left-hand one they are entirely suppressed. Found in woods at Winnipeg. Natural size.

submerged gill ridges overgrown and covered by a superficial development of the hyphae of the parasite. There is therefore a pyrenomycetous perithecia-containing stroma covering the aborted gills of the agaric and thus adding to the thickness of the flesh.

The parasitised fungus, when full-grown, instead of emitting a cloud of basidiospores, emits a cloud of ascospores (Fig. 19, A). I gathered some fruit-bodies, took them to the laboratory, and

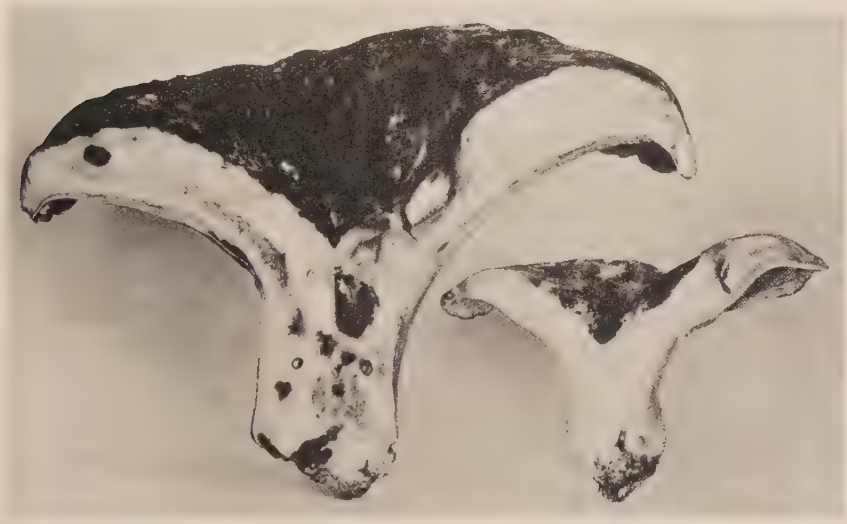


FIG. 18.—Vertical sections through two fruit-bodies of *Lactarius piperatus* attacked by *Hypomyces lactifluorum*. The gills are undeveloped. The under side of the pileus is thickly dotted with perithecia. Found in woods at Winnipeg. Natural size.

placed them in their natural upright positions in a large glass damp-chamber. On the next day, I removed one of them and so placed it in still air that a beam of sunlight passed underneath its pileus. Immediately I perceived that the Hypomyces was discharging its spores. A steady thin cloud of spores, every spore glistening in the sunlight, was maintained for some time. While some of the spores were being borne away by slight air currents, others newly ejected took their place beneath the pileus, so that the cloud was constantly rejuvenated. The distribution of the perithecia was about nine to each square millimetre of pileus surface (Fig. 19, B) ; and, since the area beneath the pileus covered

by the perithecia was about 2,500 square mm., the number of separate perithecia must have been about 20,000. Each active perithecium was discharging eight ascospores from a single ascus at short intervals of time, and thus, collectively, the perithecia were liberating enough spores to form the thin spore-cloud visible to the naked eye. It was observed that each ascus jet, like that of a Peziza,[1] broke up immediately after being shot outwards, so that the eight spores separated from one another and came to float separately in the air (Fig. 19, A). An examination of a spore-deposit showed that the spores were lying apart from one another and therefore had fallen as individuals and not in heaps of eight.

The number of spores produced by the parasite is considerable, as the following calculation will show. A fruit-body with a diameter of about 4 inches gives rise to about 20,000 perithecia, and each perithecium contains several hundred asci. Let us assume that, on the average, there are 400 asci in each perithecium. There are 8 spores in each ascus. The total number of ascospores produced on the under side of the parasitised fruit-body will therefore be about $20{,}000 \times 400 \times 8$ or 64,000,000. It is clear, therefore, that every parasitised fruit-body liberates many millions of spores and that the largest fruit-bodies, *i.e.* those which are 4–5 inches in diameter, liberate upwards of 50,000,000.

The discharge of the ascospores from the mouths of the numerous perithecia of a single parasitised Lactarius continues for several days. Some fresh fruit-bodies in which spore-discharge was apparently just beginning were collected in a wood and set upright in a large glass damp-chamber in the laboratory. Some black paper was then placed underneath the pilei; and the paper was changed daily. During the first four or five days a thick white spore-deposit collected on the paper; but, after this, the daily deposit grew thinner until it ceased to be produced. I came to the conclusion that, under favourable conditions, the length of the spore-discharge period of the parasite on a single Lactarius is normally from one week to ten days, *i.e.* about the same length as the spore-discharge period of many Agaricaceae[2] and, not improbably, of an unparasitised *Lactarius piperatus*.

[1] *Cf.* vol. i, 1909, pp. 234–236.

[2] *Cf.* vol. i, 1909, pp. 102–104.

In order to determine the interval of time between the discharge of successive asci from a single perithecium and also whether or not an ascus, just before it bursts, protrudes at the mouth of the perithecial neck, I proceeded as follows. I took a piece of the pileus of a Lactarius which had been kept in a large damp-chamber, placed it on the base of a compressor cell so that the red stroma of the parasite looked upwards, set the lid on the cell, and then pushed the lid downwards until its cover-glass actually touched the surface of the piece of fungus and pressed here and there against some of the more prominent perithecial necks. The cover-glass was so close to the other necks, all of which were directed upwards, that, if an ascus before its discharge had protruded far beyond the mouth of the perithecium to which it belonged, unavoidably it would have touched the cover-glass. It was observed with the microscope that every now and then groups of eight spores, together with a certain amount of cell-sap, suddenly appeared on the under side of the cover-glass just above the mouths of the necks of certain perithecia. These ascus-contents arrived at their destination without my receiving any preliminary warning that they were about to be shot away from the perithecia concerned. The mouths of all the perithecia were found to be very small—of about the same width as the diameter of an ascus—and more or less concealed by short hairs springing from the wall of the upper part of the neck-canal (Fig. 19, D and E). No ascus, even just before the discharge of its spores, ever pushed its way up the neck-canal sufficiently far to show its free end outside the perithecium.[1] Owing to the perithecial wall being opaque, I was unable to observe directly what was happening inside a perithecium during the discharge of the spores ; but, guided by analogy with other Pyrenomycetes, we may suppose it to be as follows. The

[1] Under abnormal conditions, one or more asci are sometimes squeezed out through the mouth of a perithecium. This occurred when I exposed a piece of pileus so that the red stroma dried rapidly at the surface (Fig. 19, K). The contraction of the stroma caused each perithecial chamber to diminish in volume, the wall of a chamber thus being caused to press upon the closely-packed asci within. When the pressure upon the ascus-mass attained a certain degree, several asci were often quickly passed outwards through the perithecial neck-canal. Such extruded asci were never seen to discharge any spores.

asci were elongating and swelling in succession, thus filling the perithecial chamber. The ripest ascus was elongating to about twice its original length and pushing its free spore-carrying end up into the canal of the perithecial neck (Fig. 19, F). At the same time, other asci in the perithecium were elongating also. Almost as soon as the ripest ascus had raised its free end some way up, but not the whole way, into the neck-canal, its end burst and the eight spores, together with some ascus sap, were squirted through the end of the neck-canal like a bullet through the barrel of a rifle. The ascus, after bursting, immediately contracted and sank down in a collapsed condition within the perithecium. Whereupon, the firing position at the mouth of the perithecium was taken up by another ascus which, after elongating and pushing its free end into the neck-canal, discharged its projectile in its turn, only to make way for a third ascus ; and so forth until all the asci had exploded.

To find out how often a perithecium fires off an ascus, it was only necessary to concentrate one's attention on one particular perithecium and to observe how often a group of eight spores was delivered to the under side of the cover-glass which was just above the perithecial mouth. The following observations were made on three separate perithecia.

Frequency of Ascus-discharge from a Single Perithecium.

Perithecium.	Number of Asci discharged.	Total Time for all Discharges.	Average Time between successive Discharges.
No. 1	7	7 mins. 10 secs.	1 min. 1 sec.
No. 2	4	6 mins.	1 min. 30 secs.
No. 3	6	10 mins.	1 min. 40 secs.
Totals . .	17	23 mins. 10 secs.	1 min. 21 secs.

From these data we can conclude that a very active perithecium may discharge its asci at about the rate of one a minute, but that the average rate of discharge under laboratory conditions is about one ascus every minute and twenty seconds. If there were 1,000 perithecia all active together and all liberating spores

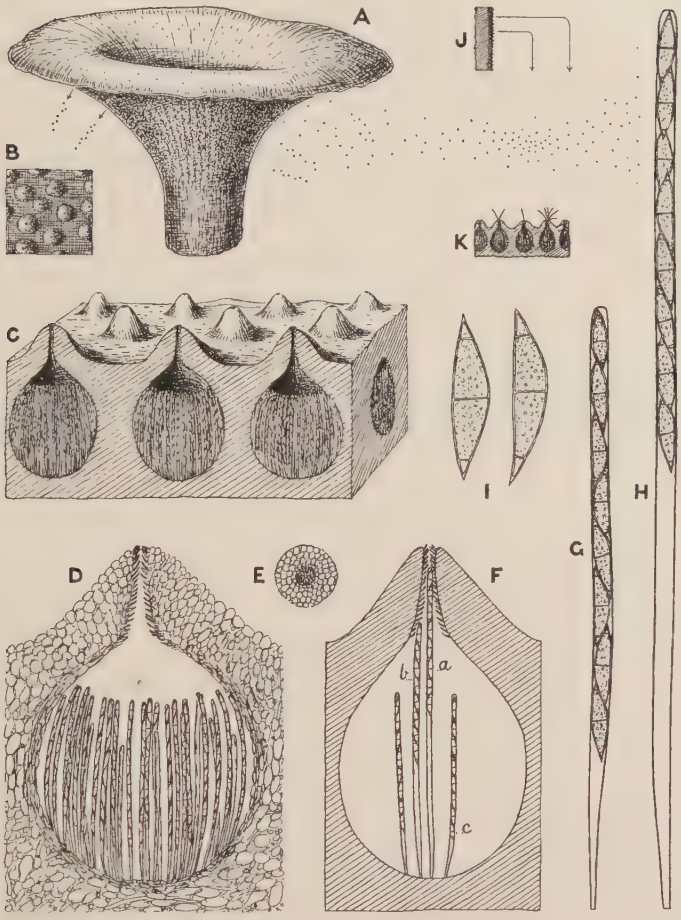


FIG. 19.—*Lactarius piperatus* parasitised by *Hypomyces lactifluorum*. A, a small parasitised fruit-body of *L. piperatus*: its gills have not been developed, owing to the attack of the Hypomyces; the under side of the pileus is thickly dotted with the red perithecia; on the right a cloud of ascospores shot out of the perithecia is being carried off by the wind, and on the left, as indicated by the arrows, two asci have just discharged their ascospores. B, one square millimetre of the under surface of the pileus enlarged, showing the protruding perithecial necks. C, a block of tissue from the under side of the pileus, showing the cavities of three perithecia containing ripening asci. D, a semi-diagrammatic section through a perithecium, showing asci ripening their spores and the narrow perithecial neck lined by hairs. E, the neck of a perithecium seen from above at the moment before an ascus is discharged: small hairs cover the mouth, and completely hide the end of the ascus about to explode. F, a diagram showing a vertical section through a perithecium and a few of the asci: *a*, an ascus, after elongation, in the firing position; *b*, another ascus elongating and preparing to take the place of *a*; *c*, an ascus before elongation. G, an ascus before elongation, showing the eight spores. H, an ascus after elongation. I, two spores, isolated. J, a block of tissue from the under side of the pileus so placed that the perithecia are directed horizontally; the two arrows indicate the sporabolic trajectories of the spores in still air, the shorter arrow showing the average distance to which a spore is projected and the longer one the maximum distance. K, a block of tissue from the under side of the pileus, which after isolation has been allowed to dry rapidly: several asci have been extruded bodily through the narrow perithecial necks. Magnifications: A, natural size; B, 11; C, 38; D, E, and F, about 67; G and H, 293; I, 462; J, natural size; K, about 5.

at the average rate observed, then 8,000 spores would be set free in 80 seconds, *i.e.* at the rate of 100 per second. This would be sufficient to produce a thin continuous cloud such as one sees in a beam of sunlight directed beneath an active fruit-body.

The distance to which the ascospores are shot in still air, before their velocity of propulsion is reduced to zero by the resistance of the air, is from 0·5 to a little more than 1 cm. (Fig. 19, J). This was proved by two experiments. In the first, a piece of pileus having a superficial area of about 2 square cm. and a thickness of 4 mm., was placed with the necks of the perithecia looking vertically upwards in a large compressor cell. The lid of the cell was then inverted and laid over the base in such a way that the cover-glass of the lid was raised just 1 cm. above the necks of the perithecia. The preparation was left undisturbed during a night. Next morning it was found that a number of ascospores had been shot up to the cover-glass and had stuck there, but that the majority of the spores discharged from the asci were lying over the perithecial stroma in the form of a white spore-dust. Since newly-discharged ascospores always stick to glass when they strike it, the experiment showed that, while some of the asci of the Hypomyces can shoot their spores 1 cm. or more high, the majority of asci cannot do this. In a second experiment, a piece of pileus was placed on the base of a van Tieghem cell so that the perithecial layer was in a vertical plane, and then a cover-glass was sealed on to the glass ring with vaseline. The preparation was therefore arranged so that the asci would shoot out their spores horizontally in still moist air and so that the spores, as soon as the resistance of the air had reduced their propulsion velocity to zero, would fall on to the horizontal base of the cell. After a night had passed, the preparation was examined, and it was found that the spore-deposit was thickest about 0·5 cm. from the perithecial layer and that, proceeding away from this layer, the deposit grew thinner and thinner until, at a distance of a little more than 1 cm., its limit was reached. From these experiments, we may draw the conclusion that the spores are violently propelled from the necks of the perithecia to a distance of from 0·5 cm. to 1 cm. before their velocity of propulsion is reduced to zero by the

resistance of the air. There is no doubt that the trajectory of each one of these ascospores is a sporabola and in general form resembles that of *Psalliota campestris* and of *Amanitopsis vaginata* of which illustrations are given in Volume I.[1]

The ascus-apparatus for discharging projectiles is not so delicate as the basidial. From a sterigma of a basidium the spore is usually shot only about 0·1–0·2 mm., but from a normal ascus, where the eight spores must be squirted out in a jet together, the distance of discharge is in general not less than 0·5 cm., often 1–3 cm. (Pezizae, etc.), and sometimes as much as 35 cm. (*Ascobolus immersus*).[2] We may regard the normal ascus, therefore, as an apparatus which, by the very nature of its construction, while unfitted for propelling its spores so small a distance as 0·1–0·2 mm., is admirably fitted for shooting them to a distance of the order of 1 cm. Now this fact is correlated, so it seems to me, not only with the entire absence of narrow hymenial tubes, closely packed gills, closely packed spines, etc., in the fruit-bodies of the fleshy Ascomycetes, but also with the suppression of the gills in our parasitised *Lactarius piperatus*. Let us suppose for a moment that in the parasitised fruit-body of this species the gills were not suppressed but were crowded together in the normal manner, with interlamellar spaces varying from about 0·5 mm. to 1–2 mm. in width; and let us further suppose that the perithecial stroma completely covered these gills, so that the mouths of the perithecia looked horizontally into the interlamellar spaces. Then, the mouths of the perithecia would be so near to the opposing gills that the asci would shoot their spores right across the interlamellar spaces, and the spores, owing to their adhesiveness, would stick to the gills which they struck. The consequence of this would be that very few of the discharged ascospores would ever fall into the interlamellar spaces and thus escape from the fruit-body, and the dissemination of the spores of the parasite by the wind would be rendered practically impossible. From these considerations we see that the suppression of the gills of the parasitised Lactarius is a condition of the greatest importance to the welfare of the parasite, and that this suppression is therefore fraught

[1] Vol. i, 1909, p. 185. [2] *Ibid.*, p. 252.

with a most beautiful biological significance. In the morphogenic effect of the Hypomyces upon its host we have something analogous to the action of gall-insects in moulding the leaves and stems of Flowering Plants into food pockets, strong boxes, etc., *i.e.* into such forms as physically appear to be best adapted to suit the requirements of the larvae.

It is interesting to compare the attacks of *Ustilago tritici* upon a Wheat plant, and of *Hypomyces lactifluorum* on Lactarius. In both cases, the parasite takes up its residence in that part of its host to which food materials normally flow in large quantities for storage in the reproductive bodies. These food materials are then appropriated, so that those which would normally go to fill the endosperm of the Wheat grain eventually come to fill the chlamydospores of the Ustilago, while those which, in the ordinary course of events, are destined to be stored in the basidiospores of the Lactarius, eventually find themselves in the ascospores of the Hypomyces. The parasites do not kill their host-plants or diminish their vigour, but they render them quite sterile, so that the Wheat plant ripens not a single grain and the fruit-body of the Lactarius not a single spore. The Smut Fungus produces its chlamydospores in the organs of dissemination of its host : it prevents the proper development of the embryo and endosperm, but the pericarp is less affected so that it constitutes a protective chamber-wall whilst the chlamydospores are in course of formation. The Hypomyces prevents the development not only of the hymenium of the Lactarius but also of the gills. On the other hand, it builds its own chambers, the pear-shaped perithecia, in which it may produce its ascospores. To sum up, one may say that both of the host-plants are completely mastered by their respective parasites.

In conclusion, it may be remarked that the parasitised Lactarius fruit-bodies are edible. Cut up into pieces and set in a dry place, they quickly dry up and then form hard masses reminding one of slices of dried apples. In this state the fungus can be preserved indefinitely. At Winnipeg, Galician immigrants and others collect the fruit-bodies in late summer, cut them up, dry them in the sun, and store them in bags for the winter. One such immigrant said that, when he desires to cook the fungus in winter-time, he takes

a handful of the slices, soaks them in water, boils them for a short time to soften them, and then fries them in butter for a few minutes. For this particular immigrant the parasitised Lactarii afforded a favourite food, and he said that he would rather have a dish of them than a good sirloin steak. I suspect, however, that the last statement proceeded from pride of special culinary knowledge and was intended rather to impress the hearer than to convey exact truth. I myself have eaten of the fungus. I find it pleasant to the taste but not so good as the Field Mushroom (*Psalliota campestris*).

Sterile Fruit-bodies.—Already in Volume I, some remarks were made upon the occasional sterility of Coprinus fruit-bodies. It was pointed out that certain fruit-bodies which otherwise appear to undergo perfectly normal development, fail in their essential function of producing spores.[1]

Occasional sterility of fruit-bodies seems to be a phenomenon by no means limited to the Coprini but to be widely spread throughout the Hymenomycetes. The first observations concerning it were made by Léveillé upon *Lactarius vellereus* in his classical researches on the structure of the hymenium. He says: "Once I found a complete abortion of the organs of fructification in *Agaricus vellereus*; the surface (of the hymenium) was smooth, and uniform, and exhibited neither basidia nor cystidia. It was quite impossible to find spores or any bodies comparable with these organs."[2] Stevenson remarks that *Stropharia obturata* Fr. has gills which "often become sterile and remain white, so that it may be easily taken for a species of Armillaria."[3] The so-called *Clitocybe Sadleri*, represented in Plate 127 of Cooke's *Illustrations*, which has lemon-yellow gills, is now generally recognised as being nothing more than a sterile form of *Hypholoma fasciculare*. It has been found by Miss E. M. Wakefield and W. B. Grove not infrequently on stumps in the herbaceous grounds of Kew Gardens.[4] Fries states that in *Russula integra* the gills are sometimes quite

[1] A. H. R. Buller, *Researches on Fungi*, vol. i, 1909, pp. 15–17.

[2] J. M. H. Léveillé, "Recherches sur l'Hyménium des Champignons," *Ann. Sci. Nat.*, 2 sér., Botanique, T. VIII, 1837, p. 327.

[3] J. Stevenson, *British Fungi* (*Hymenomycetes*), vol. i, p. 311.

[4] *Cf.* Massee, *British Fungus-Flora*, vol. ii, p. 442.

sterile and hence remain persistently white.[1] Grove has found sterile specimens of *Stropharia semiglobata*[2] and of *Paneolus campanulatus*.[3] In the latter species he found that the hymenium contained basidia which projected beyond the paraphyses, that a number of the basidia possessed four sterigmata, but that spores were entirely absent.

The new observations to be recorded here concern *Coprinus lagopus* (= *C. fimetarius*). It was found that, when this species is cultivated in pure cultures of polysporous origin on sterilised horse dung in the laboratory, sterile fruit-bodies sometimes appear among the fertile ones. Normal spore-bearing fruit-bodies (Fig. 20) have pilei which turn grey just before expansion owing to the spores developing a very dark pigment in their walls. A quite sterile fruit-body (Fig. 21) never turns grey but remains yellowish-white except at the disc which is brownish. There are degrees of sterility, for some fruit-bodies were observed which were quite sterile, some which were sterile in the lower half of the expanded pileus, some in the upper half, while some were sterile on one side of the pileus only. Moreover, certain fruit-bodies, which were completely yellowish-white and appeared to the naked eye to be quite sterile, were found with the aid of the microscope to have developed spores on a very few basidia scattered here and there in the hymenium.

Completely sterile fruit-bodies, except for their colour, appear to be quite normal in external appearance. They attain normal size, their pilei expand with the usual rapidity, and the phenomenon of autodigestion of the gills is well exhibited (*cf.* Figs. 20 and 21). As the gills disappear, drops of a yellowish juice collect at the periphery of the pileus under moist conditions. The fact that autodigestion occurs in these sterile fruit-bodies is interesting, because it proves that the process of autodigestion in normal fruit-bodies is not initiated or controlled by the ripening or the discharge of the spores.

An examination of the gills of a completely sterile fruit-body

[1] E. Fries, *sec.* Stevenson, *loc. cit.*, p. 128; and Massee, *British Fungus-Flora*, vol. iii, p. 41.

[2] W. B. Grove, "The Flora of Warwickshire," *Fungi*, 1891, p. 419.

[3] W. B. Grove, "An Agaric with Sterile Gills," *Nature*, vol. lxxxv, 1910, p. 531.

with the microscope revealed the fact that basidia and paraphyses are developed in the hymenium in the usual numbers (Fig. 22,

FIG. 20.—Two normal fruit-bodies of *Coprinus lagopus* (= *C. fimetarius*) grown on horse dung in the laboratory. In both, the pilei were grey owing to the presence of the black spores upon the gills. The left-hand one, which is beginning to expand, has not yet begun to shed spores. The right-hand one has already shed a great many spores, some of which have settled on the middle part of the stipe. Natural size.

A and B). The basidia are dimorphic, the long ones and the short ones being distributed in the normal manner (Fig. 22, B and C).

However, none of the basidia produce sterigmata or spores. The hymenium therefore presents the appearance of having been developed quite normally up to a certain stage, and of then having had its development arrested.

Cystidia develop in the sterile fruit-bodies in the normal manner,

FIG. 21.—Some sterile fruit-bodies of *Coprinus lagopus* (= *C. fimetarius*) grown on sterilised horse dung in the laboratory. The pilei were yellowish-white, owing to the gills being white on account of the absence of spores, and owing to the presence of a yellowish-brown pigment in the pileus-flesh toward the apex. The expanding fruit-body lying horizontally in the foreground should be contrasted with the left-hand fruit-body of Fig. 20. Natural size.

i.e. they grow to the normal size, acquire the normal shape and, before the expansion of the pileus, are firmly attached to both of the opposing gills, so that they form a series of bridges across the interlamellar spaces (Fig. 22, C). Cystidia, in normal fruit-bodies of Coprini, always develop very early and attain full size before the basidia give birth to spores. Since the basidia of our sterile fruit-bodies do not have their development arrested until the moment

when they should proceed to the construction of the spores, it is not surprising that the cystidia do not differ in appearance from those which are present in fertile fruit-bodies.

The cause of the arrested hymenial development for the present is a mystery. It cannot be the action of a parasite, because sterile fruit-bodies make their appearance in pure cultures ; and it cannot be a deficiency of food material in the substratum, for sterile fruit-bodies come up in pure cultures on fresh sterilised horse dung.

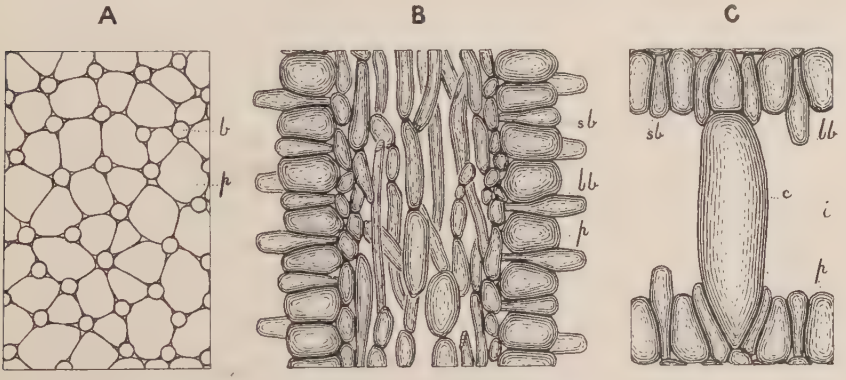


FIG. 22.—The histology of a gill of a sterile fruit-body of *Coprinus lagopus* (= *C. fimetarius*). A, optical section through the hymenium parallel to its surface ; *b*, a basidium ; *p*, a paraphysis. B, cross-section through part of a gill : the hymenium contains long basidia, *lb* ; short basidia, *sb* ; and paraphyses, *p*. C, a cross-section through the hymenium of two adjacent gills before the expansion of the pileus : a cystidium, *c*, of normal size is stretched across an interlamellar space, *i* ; *lb*, a long basidium ; *sb*, a short basidium ; *p*, a paraphysis. Magnification, 293.

Coprinus lagopus is heterothallic. In her plate cultures of this fungus Miss Mounce, working in my laboratory, observed that the fruit-bodies arising from a secondary (diploid) mycelium produced by the union of two primary mycelia of opposite sex were perfectly fertile and appeared soon after the mating of the two primary mycelia had been effected, whereas the fruit-bodies arising from unmated primary (haploid) mycelia were sterile and developed tardily.[1] Here, therefore, fertility was associated with the diploid condition of the mycelium and sterility with the haploid.

A great many spores of *Coprinus lagopus* were sown together on

[1] *Vide infra*, vol. iv, Chap. III.

sterilised horse dung contained in large crystallising dishes covered with glass plates; and the dishes were kept in the light on a laboratory table. The mycelium of these polysporous cultures, undoubtedly, must have been secondary (diploid) in character, owing to the union of primary mycelia of opposite sex. Yet among the numerous, grey, perfectly fertile fruit-bodies produced in the course of two or three weeks a few equally large, yellowish-white, sterile fruit-bodies always made their appearance. Here, therefore, the sterility cannot be associated with the haploid condition of the mycelium, but must be due to some other factor. Perhaps this other factor is too great a luxuriance in the production of fruit-bodies. On unsterilised horse dung, under natural conditions, the fruit-bodies of *Coprinus lagopus* are usually not so crowded or so large as in the artificial cultures just described, and usually they are all fertile. In the artificial cultures the lack of competition with other organisms results in the coming to maturity of a larger number of rudimentary fruit-bodies than normally occurs in nature. Thereby the balance between the capacity of the mycelium for supplying growth materials to the fruit-bodies on the one hand and the size and number of the fruit-bodies actually produced on the other hand may be upset, so that some of the fruit-bodies do not obtain the quantity of growth materials requisite for their full development and suffer partial starvation when just about to expand. Possibly, therefore, the imperfect development of the hymenium in some of the fruit-bodies is simply due to lack of vigour brought about by imperfect food supply from the mycelium. An analogy, perhaps, is to be found in Apple trees which often set many more fruits than they can possibly bring to perfection. When this happens, as is well known, many of the apples cease their development when about one-quarter grown and, whilst still green and sour, fall to the ground. The half-developed fruit-bodies in the sterile cultures of *Coprinus lagopus* perhaps compete for the materials necessary for their development held within the mycelium much in the same way that the partially developed apples upon an Apple tree compete for the materials necessary for their development held within the twigs, with the result that some are beaten in the struggle and only undergo imperfect development.

The Monstrous Fruit-bodies of Polyporus rufescens.—*Polyporus rufescens*, of which some normal fruit-bodies are shown in Fig. 24, is remarkable in that it sometimes produces large, more or less spherical, monstrous fruit-bodies, like those shown in Fig. 23.[1] Mr. Burtt Leeper has informed me that near Salem, in the State of Ohio, while normal and monstrous fruit-bodies are found together, he has seen several hundred monstrous fruit-bodies about a stump without a single fully developed one, and that he has also seen several normal fruit-bodies in a group without the admixture of a single monstrous one.

It may be asked : how is it that *Polyporus rufescens* sometimes gives rise to normal fruit-bodies and sometimes to monstrous ones ? The answer to this question is to be found, perhaps, in the response or non-response of the fruit-bodies to the morphogenic stimulus of gravity. The form of a normal fruit-body is largely controlled by gravity. The stipe is negatively geotropic, the pileus diageotropic, the hymenial tubes positively geotropic ; and the dorsiventrality of the pileus, including the development of the hymenial tubes on the under surface, and not on the upper, is in all probability here, as in other Polypori, decided by a morphogenic stimulus of gravity. The stimulus of gravity, possibly, may influence the development of a fruit-body in further even more subtle ways than any we have yet perceived. Let us now imagine a fruit-body which, for some reason or other, has lost its power of responding to the various stimuli of gravity during its development. Then, surely, the fruit-body could become nothing other than monstrous. In the absence of control by external stimuli, it would certainly take on an unusual form. Perhaps, on enlarging, it would grow centrifugally and thus develop into a more or less spherical ball, and its hymenial tubes might come into existence irregularly all over its surface or mixed up with the fruit-body flesh, in the manner shown in Fig. 23. I am therefore inclined to think that the monstrous fruit-bodies of *Polyporus rufescens* owe their peculiar form to the loss of their

[1] *Polyporus abortivus* Peck appears to be a synonym for *P. rufescens* Fr. Peck (*Bot. Gaz.*, vi, 1881, p. 274) noticed the monstrous fruit-bodies and called them *P. abortivus* var. *subglobosus*. Of this variety he says : "Plant consisting of a depressed or subglobose mass, having the stem very short or obsolete, the central substance marked by concentric zones and the surface everywhere porous."

FIG. 23.—*Polyporus rufescens*. Two abnormal fruit-bodies in which the stipe and pileus have not been differentiated from one another and in which irregular hymenial tubes occur all over the surface. The irregular form may be due to the failure of the fruit-bodies to respond to geotropic stimuli. Photographed at Salem, Ohio, U.S.A., by Burtt Leeper. Natural size.

power of responding to certain stimuli, particularly that of gravity.[1]

The Grafting of Fruit-bodies.—In 1911, Weir found by experiment that, when a young stipe of *Coprinus lagopus* (his *Coprinus*

Fig. 24.—*Polyporus rufescens.* Several normal somewhat confluent fruit-bodies springing from fleshy-soft bases. The stipes exhibit negative geotropism, the pilei diageotropism, and the hymenial tubes positive geotropism. Photographed at Salem, Ohio, U.S.A., by Burtt Leeper. Natural size.

niveus) is grafted on to the stump of another stipe of the same species, a union quickly takes place and the pileus expands in a

[1] It would be interesting to make a cytological comparison of normal and abnormal fruit-bodies. The number, arrangement, or size of the nuclei in the abnormal form may possibly be different from that of the normal form.

normal manner. Similarly, he found that the young pileus of *Pleurotus ostreatus* can be successfully grafted on to the stipe of another fruit-body of the same species.[1] I have succeeded in a similar experiment with *Coprinus sterquilinus*. Two young fruit-bodies of this species, A and B in Fig. 25, were coming up simultaneously on sterilised horse dung kept in a dish in the laboratory. The upper halves above the dotted line were then removed with the help of a scalpel and interchanged. At C is shown the upper half of A set on the lower half of B. Union of scion and stock in this combination quickly took place, so that normal growth was resumed. Three days and six hours after the grafting had taken place, C presented the appearance shown at D. The place of union of the scion and stock is indicated by a slight constriction in the middle of the basal bulb. On the fourth day the stipe rapidly elongated, the large pileus expanded, the gills underwent autodigestion, and the hymenium discharged a vast quantity of spores in the normal manner. The other combination, *i.e.* the upper half of B with the lower half of A, failed to develop and withered without increasing in size.

Weir states that he successfully grafted young fruit-bodies of *Coprinus lagopus* (his *Coprinus niveus*) on the stipes of *Coprinus macrorhizus* (his *Coprinus fimetarius* var. *macrorhizus*), and *vice versa*; and also that he caused *Stereum hirsutum* to grow like a parasite upon *Stereum purpureum*.[2] His photographs clearly show that he erred in the nomenclature of one of his species of Coprinus. The hairs on the surface of what he calls *Coprinus niveus* prove that he was not dealing with that species.[3] There is no doubt in my mind, judging by his illustrations, that what he called *Coprinus niveus* was really the very common species *Coprinus lagopus* which is distinct from, although closely related to, *Coprinus*

[1] J. A. Weir, "Untersuchungen über die Gattung Coprinus," *Flora*, Bd. CIII, 1911, pp. 301–304.

[2] *Ibid.*, pp. 305–312.

[3] The pileus of *Coprinus niveus* is covered with white meal consisting of loose spherical cells, whereas the pileus of *C. lagopus* (= *C. fimetarius*) is adorned with thin fibrillar scales consisting of chains of elongated cells. I have grown both of these species in pure cultures on horse dung and am familiar with their appearance and structure.

macrorhizus. What Weir therefore seems to have done is to have succeeded in grafting two very closely related species of Coprinus upon one another. I have not attempted to confirm his particular

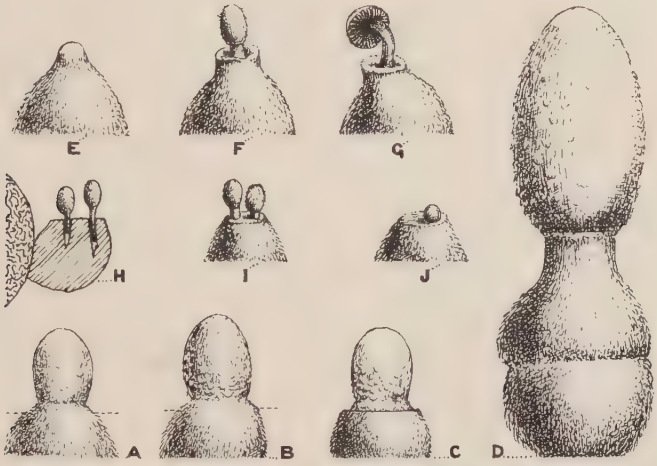


FIG. 25.—Experiments upon grafting. A and B, two young fruit-bodies of *Coprinus sterquilinus*. Both were decapitated by cutting in the direction shown by the dotted lines, and the upper parts were interchanged. C shows the bulb of A with the pileus of B set upon it. D, the same combination three days later: the scion and stock have become perfectly united and normal growth is taking place; the constriction in the bulb indicates the plane of union. E, a young fruit-body of *Coprinus sterquilinus*. A young fruit-body of *Coprinus lagopus* (= *C. fimetarius*) was set upon E after decapitation as shown at F. G is F two days later: the union has not been completed, but the scion has expanded to some extent. H, two young fruit-bodies of *Coprinus narcoticus* set in slits in a decapitated bulb of *Coprinus sterquilinus* attached to horse dung. I, to the left a fruit-body of *C. narcoticus*, and to the right one of *C. lagopus* (= *C. fimetarius*) set on a decapitated bulb of *C. sterquilinus*. J, a young fruit-body of *Coprinus echinosporus* set on a decapitated bulb of *C. sterquilinus*. The unions in H, I, and J were unsuccessful, but in H one of the fruit-bodies finally elongated its stipe and partially expanded its pileus. All natural size.

experiments but, on the contrary, have sought, as opportunity presented itself, to cause a union between two distantly related species. The nature of the experiments can best be elucidated by reference to Fig. 25. At E is a young fruit-body of *Coprinus sterquilinus*. Its rudimentary pileus was decapitated and a young fruit-body of *Coprinus lagopus*, the stipe of which had been cut transversely, was set upon its bulb, as shown at F. An

intermingling of the hyphae of the two species took place, so that the scion did not wither. After a few days the stipe feebly elongated, the pileus partially expanded, and collapse soon followed without the shedding of any spores. The expanded and collapsing fruit-body is shown at G. There is no evidence that food materials passed from the bulb of *Coprinus sterquilinus* to the stipe and pileus of *Coprinus lagopus*. This attempt at making a graft cannot therefore be said to have been successful. At H is shown the method by which another experiment was carried out. The young pileus of a fruit-body of *Coprinus sterquilinus* (*cf.* E) was first removed. Then two small slits were made in the bulb, and the upper parts of two young fruit-bodies of *Coprinus narcoticus* were placed in them. At H the bulbous base of *C. sterquilinus* is represented in vertical section attached to a ball of manure. The hyphae of the bulb enveloped the inserted stipes. One of the young scions withered without undergoing any further development. The other succeeded in elongating its stipe to the length of about an inch and in opening an abnormally small pileus, but its dwarf appearance indicated that it had received from the stock to which it was attached little or nothing more than a supply of water. At I, the two scions are the tops of young fruit-bodies of *Coprinus narcoticus* (to the left) and *Coprinus lagopus* (to the right), and at J the scion is the upper part of a young fruit-body of *Coprinus echinosporus*,[1] while the stock in both I and J is a bulb of *Coprinus sterquilinus*. In another experiment, not here represented by a Figure, a very rudimentary pileus (like that at E) of *Coprinus sterquilinus* was cut off and placed on the stump of a young stipe of *Coprinus echinosporus*. In all these experiments no successful union took place. The grafting failed. The hyphae of the scions and stocks grew together somewhat, and the scions remained fresh-looking for two or three days; but the scions eventually died without growing any larger. In the last combination attempted (pileus of *Coprinus sterquilinus* on stipe of *Coprinus echinosporus*), the scion kept its fresh appearance for five days, although after that time it began to wither. It is clear

[1] For a description of this new species, *vide* A. H. R. Buller, "Three New British Coprini," *Trans. Brit. Myc. Soc.*, vol. vi, Part IV, 1920, p. 363.

from all that has just been said that the attempts to graft together species of Coprinus which are not closely related only resulted in failure.

The confluence of fruit-bodies of one and the same hymenomycetous species—a phenomenon allied to the artificial grafting together of parts of two fruit-bodies of one and the same species —may sometimes be observed in woods and fields. In many Polyporeae, the pilei often become confluent where they happen to come in contact during their peripheral extension. Thus, in *Polystictus perennis*, one not infrequently finds two or three fruit-bodies which have a large compound pileus in common but two or three independent stipes, so that one is reminded of the Indian Banyan tree with its vertical roots supporting the far-spreading branches. Again, *Amauroderma salebrosum*, an African Polypore, often develops fruit-bodies with fused pilei. Thus in the Herbarium at Kew there is a specimen with two long cylindrical independent stipes and one round compound pileus, the two halves of the pileus evidently representing the two originally separated pilei. In the Agaricineae, on the other hand, confluent pilei only occur as abnormalities and are comparatively rare. Figure 26 shows two confluent pilei of *Psathyrella disseminata*. The rudiments of the fruit-bodies appear to have originated in the closest proximity, so that possibly the confluence of their pilei and stipe-bases was caused simply by mutual pressure.[1] Where, in the Agaricineae, two pilei become confluent at an early stage of development and one of the fruit-bodies grows more vigorously than the other, the

FIG. 26. — An abnormality in *Psathyrella disseminata*. The two large fruit-bodies have confluent stipe-bases and confluent pilei. Found near Birmingham, England. Photographed by J. Edmonds. Natural size.

[1] A similar confluence of two large *Boletus subtomentosus* fruit-bodies is to be seen in a photograph kindly sent to me by A. F. Peck.

pileus of the less vigorous fruit-body may be dragged away from its base, and carried up on to the top of the pileus of the more vigorous fruit-body, there to continue its growth in a more or less inverted position and in a parasitic manner. Thus probably came into existence the small partially inverted pileus of *Tricholoma nudum* which is seen attached to a normal pileus in Fig. 27.[1]

Fig. 27.—*Tricholoma nudum*. Confluence of fruit-bodies. The largest fruit-body bears at its apex another fruit-body which is partially inverted. Photographed at Scarborough, England, by A. E. Peck. About $\frac{2}{3}$ the natural size.

A similar explanation may perhaps account for the strange abnormality shown in Fig. 28. Here a fruit-body of *Clitocybe nebularis* has attached to its apex two smaller fruit-bodies, one normal-looking with a centric stipe and a downward-looking pileus, and the other with a very short lateral stipe and an inverted pileus. It may be that two fruit-body rudiments were pushed up into the air upon the pileus of the large fruit-body and that they fused with the pileus upon which they were seated and continued their development in a parasitic manner, thus giving us what we see in Fig. 28. On the other hand, it is possible that we here have a case of congenital proliferation: the pileus of the large fruit-body may have grown upwards at one spot, and the abnormal tissue thus developed may have become differentiated into the two smaller fruit-bodies which the large one now sustains.[2]

The Dwarf Fruit-bodies of Coprinus lagopus.—The size of the

[1] *Cf.* W. C. Worsdell, *The Principles of Plant Teratology*, vol. i, London, 1915, p. 20.

[2] *Ibid.*, p. 21.

fruit-bodies of any Boletus or species of Agaricineae with a centric stipe varies about a mean in accordance with the law of continuous variation, and the range of variation for most of the common species, *e.g.* for *Boletus edulis*, *Amanitopsis vaginata*, *Lepiota procera*, and *Coprinus comatus*, is not very great, is roughly recorded in most fungus floras, and is well known to field mycologists. However, in *Coprinus lagopus* the range of size-variation is of unusual extent, owing to the fact that, besides producing the familiar larger fruit-bodies (Fig. 20, p. 71), this fungus gives rise, under certain conditions of nutrition, to very small fruit-bodies, some of which are less than one hundredth the size of the larger ones. These extremely small fruit-bodies will be called in what follows *dwarf fruit-bodies*. Before these dwarfs are discussed in detail, an account of a method for obtaining well-developed fruit-bodies will be first described.

FIG. 28.—An abnormality in *Clitocybe nebularis*. The largest fruit-body bears at its apex a normal fruit-body with a centric stipe and another fruit-body with a lateral stipe and an inverted pileus. Found at Northwood, Middlesex, England, in 1913, and photographed by Somerville Hastings. About natural size.

At Winnipeg, when fresh horse dung is procured from a stable and kept enclosed in a large crystallising dish in the laboratory, it usually happens that, at the end of two or three weeks' time, three or four species of Coprinus make their appearance on the dung-balls. These species are: *Coprinus lagopus*, *C. curtus*, (= *C. plicatiloides* of Vol. I), *C. ephemerus*, and

C. cordisporus.[1] Later on, if the dung is kept moist, certain other Coprini may spring up, among which may here be mentioned: *C. stercorarius*, *C. narcoticus*, and *C. sterquilinus*. The pilei of *Coprinus lagopus* are at first white and covered with a hairy veil (*cf.* the young fruit-bodies on the dung-ball in Fig. 21, p. 72) and subsequently, after expansion, cinereous grey and bearing thin, easily-rubbed-off, fibrillose scales (Figs. 20 and 21). The presence of these fibrillose scales at once distinguishes the fruit-bodies of *C. lagopus* from those of all the other species in the culture except those of the relatively gigantic *C. sterquilinus* with which we shall become acquainted in Volume III. The size of these spontaneously developing fruit-bodies is very variable indeed, the largest being about the size of those shown in Fig. 20 and the smallest less than a quarter as large; but all of them, from the largest to the very smallest, exhibit upon their pilei the characteristic, easily detachable, hairy scales. To prepare the medium for a pure culture, all that one needs to do is to take some fresh horse-dung balls, put them in a large crystallising dish, cover the dish with a glass plate, and sterilise the whole at 100° C. for one hour in a steam steriliser. This ensures the killing of all the fungus spores in the medium and most of the bacteria. To infect the medium, one takes an expanded pileus of *Coprinus lagopus* with a pair of sterilised forceps, lifts the covering plate of the dish, and holds the pileus for about half a minute over the dung-balls in succession. During this operation many spores are discharged from the gills and fall on to the dung. The plate is then replaced on the top of the dish and the culture set on a table in the laboratory. The spores germinate, the germ-tubes rapidly develop into mycelia, the mycelia soon anastomose with one another, and fruit-bodies come up on the dung-balls at the end of about three weeks. I have seen the life-cycle from spore to spore accomplished in exactly 21 days. The fruit-bodies which come up in pure cultures of the kind just described are usually much larger than those which come up spontaneously on horse dung in competition with other species.

[1] For nomenclature *vide* Jakob E. Lange's useful revision of the genus Coprinus in his "Studies in the Agarics of Denmark," *Dansk Botanisk Arkiv udgivet af Dansk Botanisk Forenig*, Part II, No. 3, 1915.

The range of variation in the size of fruit-bodies of *Coprinus lagopus* is indicated by the measurements recorded in the adjoining Table. The length of the stipe was measured after the stipe had become fully extended and the diameter of the pileus as soon as the pileus had become expanded and flattened.

Variations in Size of the Fruit-bodies of Coprinus lagopus.

Fruit-body.	Length of Stipe.	Diameter of Pileus.	Remarks.
No. 1	184 mm.	40 mm.	On horse dung in a pure culture.
No. 2	130 mm.	24 mm.	
No. 3	115 mm.	30 mm.	In the laboratory on horse dung obtained from stables and roads at Winnipeg.
No. 4	108 mm.	14 mm.	
No. 5	62 mm.	26 mm.	
No. 6	55 mm.	7 mm.	
No. 7	52 mm.	15 mm.	
No. 8	27 mm.	5 mm.	
No. 9	10 mm.	3 mm.	Dwarf fruit-bodies on horse dung in fields in England and on road dung in the laboratory at Winnipeg.
No. 10	2 mm.	1 mm.	
No. 11	1 mm.	0·75 mm.	

The largest fruit-body I have yet seen, No. 1 in the Table, had a stipe 184 mm. long and a pileus 40 mm. wide, and it came up in a pure culture ; while the smallest fruit-body I have yet seen, No. 11 in the Table, had a stipe only 1 mm. high and a pileus only about 0·75 mm. wide. This dwarf came up in company with other dwarfs a little larger than itself on a horse-dung ball obtained from a road at Winnipeg. Its height was only a one-hundred-and-eighty-fourth part of the height of the largest fruit-body which would be considered by most mycologists as typical for the species.

The dwarf fruit-bodies of *Coprinus lagopus*, with stipes only from 1 to 10 mm. high and with very minute pilei, are just as perfect functionally as large fruit-bodies. Their hymenium, it is true, is exceedingly limited in area, and produces only a few hundreds or thousands of spores ; but, as soon as the pileus expands, it liberates these spores in the normal manner.

When one compares a dwarf fruit-body with one of much larger stature, one notices differences other than that of mere size. In a

large pileus, the number of gills may exceed 100 ; but, in a dwarf pileus, this number is greatly reduced and is usually not more, and sometimes less, than 20. In a dwarf pileus, which was less than 1 mm. in diameter, the gills were very shallow and only numbered 9, with faint traces of some very short intermediate ones. The smaller the pileus, the fewer are the cystidia projecting from its gills ; and in the dwarf pileus just referred to as being less than 1 mm. in diameter there were no cystidia at all. The largest of the cells in the filaments making up the pileal scales of a dwarf fruit-body are appreciably smaller than similar cells of a large pileus. Finally, the spores of dwarf fruit-bodies, while of about the same width as those of large fruit-bodies, are distinctly shorter. The size of the cell-elements of the fruit-bodies of *Coprinus lagopus* therefore appears to be correlated to some extent with vigour of fruit-body development.

On exhausted horse-dung balls, where the competition among various fungi for food materials is very keen, the production of dwarf fruit-bodies by *Coprinus lagopus* is quite common ; and I have often met with them in fields in England. There is no difficulty in convincing one's self that these tiny fruit-bodies from 1 to 10 mm. high really do belong to the species in which they have been placed. The colour and hairy scales of the pileus, the nature of the cystidia, the intense blackness and oval shape of the spores, etc., which one observes in studying a dwarf, all point to the conclusion that the dwarf should be regarded as a product of *Coprinus lagopus* ; but the most convincing evidence that this conclusion is correct is afforded by pure cultures. I found that, when the spores of a dwarf fruit-body are sown on sterilised horse dung, large fruit-bodies are obtained with stipes upwards of 100 mm. in length and pilei from 15 to 40 mm. in width, exactly resembling typical large specimens of *Coprinus lagopus*.

The dwarf fruit-bodies under consideration are of interest not only to the physiologist but also to the systematic mycologist, for I am convinced that very frequently, on account of their small size, their true affinity has not been recognised and they have therefore been placed in a species distinct from *Coprinus lagopus*. Even Massee, who wrote a monograph on the genus Coprinus, made

this error. In the year 1911, when I was studying the specific differences of a number of coprophilous Coprini, I was uncertain which fruit-bodies were considered as being included in *Coprinus radiatus*. When at Kew, I therefore asked Massee his opinion on the matter. He said that *C. radiatus* was a very minute species very common on horse dung in pastures, and he kindly took me on a little excursion into the field adjoining the Royal Herbarium in order to find some specimens. Soon, on turning up a mass of horse-dung balls which was dry on the top and had been lying in the field for some time, he found among the crevices between the balls a number of very small fruit-bodies which were only a few millimetres high and which evidently belonged to three separate species of Coprinus ; and he then indicated the fruit-bodies which he regarded as belonging to *Coprinus radiatus*. These were of the most delicate construction, so delicate indeed that on exposure to the open air they actually did " wither with a breath " in accordance with the description of them in Massee's *Fungus Flora*. I made a careful note of the appearance of these small fruit-bodies. Their stipes were extremely thin, much less than 1 mm. thick, and from about 2 to 10 mm. high, and their pilei were from about 2 to 5 mm. in diameter. Further, the pilei were bluish-grey, flattened with a depressed disc, plicated, and here and there bearing a few patent, fibrillose, easily detachable scales. These scales and the general appearance of the pilei at once reminded me of the relatively large fruit-bodies of *Coprinus lagopus* which I had so often seen in my cultures and had studied at Winnipeg. I therefore collected the dung-balls, dried them, took them to Winnipeg, after six months watered them, then put them in a closed crystallising dish, and awaited the result. In the course of a few days, some more of the delicate fruit-bodies came up. I then examined their structure with the microscope and found it identical with that of the fruit-bodies of *C. lagopus*. Subsequently, I took the spores of a dwarf fruit-body, sowed them on sterilised horse dung, and obtained large fruit-bodies of *C. lagopus*. Thus I convinced myself that the species which Massee described in his *Fungus Flora* as " withering with a breath," under the name of *Coprinus radiatus*, is nothing more than an assemblage of dwarf fruit-bodies of *Coprinus lagopus*.

Every one knows that certain annual Phanerogams, when grown under very dry conditions, attain a very small height and bulk but that, even in this dwarfed state, they yet succeed in producing a few flowers and seeds. A few seeds, from the point of view of the maintenance of these species, are better than none at all. It seems to me that a similar consideration applies to the dwarf fruit-bodies of *Coprinus lagopus*. Under certain conditions of drought or competition with neighbouring species, only dwarf fruit-bodies are developed, but these succeed in producing and liberating a small number of spores, which are disseminated by the wind. A few spores, from the point of view of the maintenance of the Coprinus species, are better than none at all and may chance to germinate under favourable conditions. The dwarf fruit-bodies, therefore, ought not to be despised on account of their size.

Coprinus lagopus is not the only coprophilous species of Coprinus which under unfavourable conditions produces dwarf fruit-bodies, for I have observed dwarfs in both *Coprinus ephemerus* and in *C. curtus*. The dwarfs of these two last species sometimes occur along with the dwarfs of *C. lagopus* on the lower sides of drying dung-masses in fields in England and on exhausted dung in the laboratory at Winnipeg. A well-developed fruit-body of *C. ephemerus* often has a height of 30 or more mm. and a pileus width of about 10 mm. ; but one of the dwarfs of this species, which I examined at Winnipeg, had a stipe which was only 2 mm. high and 0·1 mm. thick, and a pileus only 0·4 mm. in diameter. Furthermore, the pileus possessed only 5 shallow gills with no traces of any others, and the spores produced numbered less than 1,000 ; yet this tiny fruit-body expanded its pileus and doubtless successfully carried out its spore-discharging function.

The Cultivation of Marasmius oreades for Food.—*Marasmius oreades*, the Fairy-Ring Fungus (Fig. 29, A, B, C ; also Vol. I, Fig. 39, p. 107), is one of the commonest of Hymenomycetes in pastures, on lawns, and in other grassy places. Its small tan-coloured fruit-bodies come up in rings often in large numbers, and are edible. In a warm place they rapidly dry up and, in the desiccated condition, they retain their fitness to be used as food indefinitely.

Marasmius oreades can be cultivated on manure in gardens and thus a supply of large fruit-bodies may be obtained for the table. This fact is not generally known to mycologists nor, so far as I am aware, has it found its way into botanical literature.

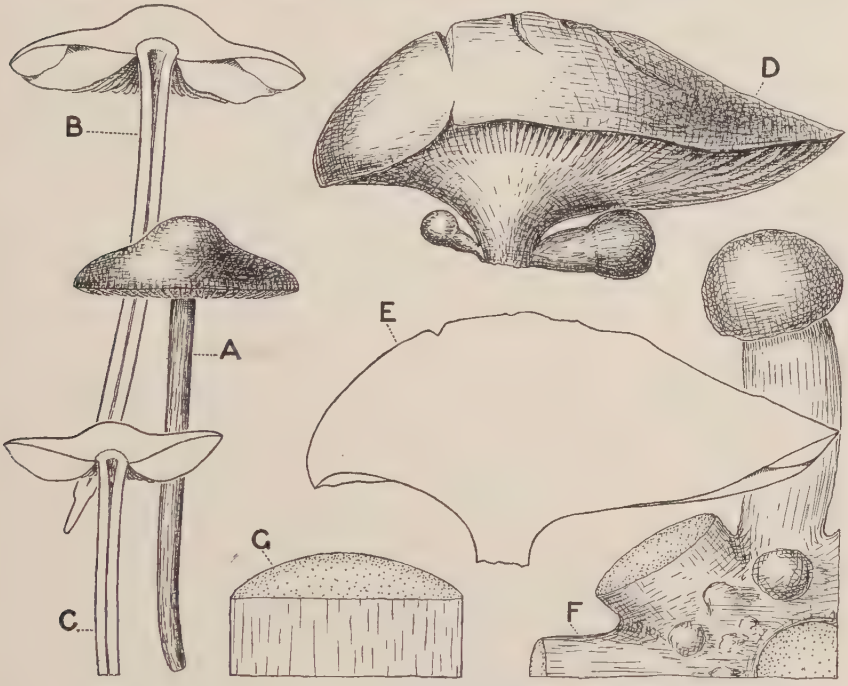


FIG. 29.—*Marasmius oreades*, wild and cultivated fruit-bodies contrasted. A, B, and C, normal fruit-bodies from a field. D, E, F, and G, abnormal fruit-bodies grown on a manure bed at Winnipeg. D, a fruit-body having a very fleshy pileus, a small stipe, and reduced gills. E, the same in vertical section (*cf.* B and C). F, part of a large cluster of fruit-bodies three of which have been cut away; the remaining fruit-body has a very thick stipe (*cf.* A, B, and C). G, a piece of one of the thickest stipes (*cf.* A, B, and C). All natural size.

I shall therefore take this opportunity of recording the results of my enquiries and observations with respect to an artificial Fairy-Ring Fungus bed which I saw at Winnipeg in the autumn of 1913.

The Fairy-Ring Fungus bed about to be described was situated in a garden (now built over) in Gladstone Street, Winnipeg, and was made by Mr. W. Maskell who, before emigrating to Canada, had been a chef in a large house in England. As a chef, he had long known how to employ the Fairy-Ring Fungus in making soups

and ragouts. As soon as my attention had been called to the bed by a paragraph appearing in a local newspaper, I communicated with Mr. Maskell and he kindly showed me the bed, told me the details of its origin, and gave me a basketful of its products.

The nutrient substratum of the bed consisted of a mixture of one load of horse manure and one load of cow manure. This mixture, in the spring of 1909, was placed in the garden so as to fill up a hollow in the ground and form a sloping bank. The mass of manure so deposited was 30 feet long, 6 feet wide, and had a maximum depth of 4 feet. The bed, after having thus been made, was covered with a layer of black garden soil 16 inches deep. The top of the bed was kept free from weeds.

The spawn with which the bed was planted originated in England and was brought to Winnipeg by a gardener, along with a few bulbs, etc., from a garden attached to a large country house in Hertfordshire. The gardener told Mr. Maskell that he had grown the fungus for years and was used to supplying the " champillions " to the house for use in the kitchen ; and he gave Mr. Maskell a lump of the spawn which was just large enough to fill the palm of his hand. A short time after the bed had been made, Mr. Maskell broke up his lump of spawn into about twelve pieces and then spawned the bed with them by setting them at intervals, 3–4 inches deep, in the manure under the layer of soil.

The bed which, as we have seen, was spawned in the spring of 1909, yielded nothing in the autumn of 1909, but began to bear in the summer of 1910. In the spring of 1911, it was thoroughly turned with the spade. This turning mixed the soil and manure, and spread the mycelium, which had developed only around the original pieces of spawn, throughout the bed. In the autumn of 1911 there was a second crop. In the spring of 1912 and also of 1913 the upper part of the bed was dug over again, and further crops of fruit-bodies were obtained in the late summer and autumn of both these years. Therefore, up to the time I saw it, the bed had borne fruit-bodies for four successive years, 1910–1913 inclusive. Mr. Maskell assured me that the crops had increased in vigour with each successive year.

I visited the bed on October 11, 1913. In this year the bed had

begun to bear in July, and it was still producing fruit-bodies when I saw it in October. Five baskets full (14 × 7·5 × 5 inches) had already been gathered during the season. Altogether, the four crops

Fig. 30.—*Marasmius oreades*. Vertical sections through four fruit-bodies grown from spawn in a manure bed at Winnipeg. (1) The fruit-body on the right is most like a normal wild fruit-body, but its stipe is abnormally thickened and its gills but poorly developed. (2) The fruit-body on the left has a long much-thickened stipe, a relatively small pileus, and extremely reduced gills. (3) The two middle fruit-bodies are stunted and their gills but feebly developed, but their pilei and stipes are extraordinarily fleshy. No such fleshy fruit-bodies ever occur under normal conditions. Natural size.

gathered in the four seasons, 1910–1913 inclusive, had filled twenty baskets. The bed had therefore proved to be a distinct success.

On looking at the bed in October, 1913, I was astonished by the large size and fantastic appearance of many of the fruit-bodies. At first I could scarcely believe that the fungus in cultivation was really the Fairy-Ring Fungus; but all doubt about this was soon

set aside, for, on searching the bed, I first found a few almost normal fruit-bodies and then a series of intermediate fruit-bodies connecting the most normal and most abnormal with one another (Fig. 30).

Many of the fruit-bodies came up in clusters (Fig. 29, F) which reminded me of the clusters on artificial Mushroom beds. One such cluster from which several large fruit-bodies had been removed weighed 11 oz. and, doubtless, if it had remained intact, it would have weighed upwards of 1 lb. There were often twelve or more fruit-bodies in a single cluster, and some of the individual fruit-bodies in the clusters were of remarkable size (Fig. 31 ; also Fig. 29, D–G). Some of the pilei were actually 5 inches in diameter and some of the stipes 1·5 inches thick ! One never sees such gigantic fruit-bodies in nature. The stipes of wild fruit-bodies are cartilaginous and hollow and so also were the stipes of the most normal fruit-bodies on the bed, but the very thick stipes of the abnormal fruit-bodies just described were solid to the centre and composed of a uniform, although slightly fibrous, flesh. The gills in the smaller more normal fruit-bodies were fairly well developed but in the abnormally large ones remarkably reduced (Figs. 29, E and 30). The abnormally large fruit-bodies with their extraordinarily thick pilei and stipes and their greatly reduced gills certainly afford a curious and striking contrast with the beautifully proportioned fruit-bodies that one finds growing wild in fairy rings.

In order to find out why the fruit-bodies were appearing in clusters, a cross-section was made through the bed with a spade. The mycelium was then traced in the form of a loose irregular white strand from a cluster at the top of the bed downwards through the bed for a distance of 16–18 inches ; but beyond this depth it could no longer be clearly followed. From these observations I gained the impression that the mycelium had luxuriated in the rich manure deep down in the bed, that it had penetrated slowly and with difficulty through the thick upper layer of the bed, and that, having at last pushed its way to the surface at a few places by means of long loose strands of hyphae, it had spent its accumulated food materials and suppressed reproductive energy in producing large clusters of abnormal fruit-bodies. The hypertrophy of the pilei and the stipes of the largest fruit-bodies thus

appears to have been correlated with the depth of development of the mycelium upon which the fruit-bodies were borne.

FIG. 31.—*Marasmius oreades*. Two fruit-bodies grown from spawn in a manure bed at Winnipeg, seen from below. The stipes are abnormally thick and the gills but poorly developed. Natural size.

The wild fruit-bodies of *Marasmius oreades* are excellent as food, and they are superior to the Common Mushroom in that they are quite free from maggots and can be kept for a long time without rotting. The fruit-bodies raised on the manure bed were just as

good to eat as wild ones and were even more satisfactory for the table on account of their larger size. The swollen stipes of the abnormally large fruit-bodies were perfectly palatable and therefore did not need to be discarded when the fruit-bodies were being prepared for the pot.

J. S. Bayliss made an investigation upon the fairy rings of *Marasmius oreades* and came to the conclusion that the fungus is a parasite. She states that the mycelium attacks the young roots of grasses and kills them by means of some toxic excretion.[1] On the other hand, Shantz and Piemeisel, who made an extended study of a number of very large fairy rings produced by several species of fungi in Colorado, are disinclined to believe that the mycelium of fairy-ring fungi is in any sense parasitic, and hold that the death of the grass-plants and other herbs in the bare zones of the rings in dry weather is simply due to excessive local drought caused by the resistance of the subjacent mycelium-infected soil to the absorption of water and the passage of water into the roots.[2] Unfortunately, these observers did not examine the living plants among which the mycelium was growing in order to find out whether or not their roots were being entered and killed by the hyphae. Now it is known that there are a number of soil-fungi (Imperfecti) which do, as a matter of fact, attack and kill some of the roots of cultivated Gramineae such as Wheat and Maize. It seems to me not unlikely, therefore, that the mycelium of certain fairy-ring fungi, such as *Marasmius oreades*, should kill roots also, and it need be no matter for surprise if the observations of Bayliss should be confirmed and extended. I wish to point out here, however, that *Marasmius oreades*, whether parasitic or not in pastures, can certainly live as a pure saprophyte under artificial conditions, for as such a pure saprophyte it lived for five years in the bed of manure at Winnipeg. The bed, as already mentioned, was kept free from weeds so that the mycelium of the fungus never once had the chance of developing at the expense of living grass-plants.

[1] Jessie S. Bayliss, "Observations on *Marasmius oreades* and *Clitocybe gigantea* as Parasitic Fungi," *Journal of Economic Biology*, 1911, vol. vi, pp. 120, 130.

[2] H. I. Shantz and R. L. Piemeisel, "Fungus Fairy Rings in Eastern Colorado and their Effect on Vegetation," *Journal of Agricultural Research*, 1917, vol. xi, pp. 236–237.

CHAPTER IV

THE DISCHARGE OF SPORES FROM CERTAIN AGARICINEAE AND POLYPOREAE

The Brief Spore-fall Period of *Coprinus curtus*—Macroscopic Observations on the Fall of Spores of *Armillaria mellea*—Banker's Observations on Spore-discharge in *Hydnum septentrionale*—The Vernal Spore-fall Period of *Fomes fomentarius*—Perennial Spore-production by One and the Same Tube-layer in *Fomes fomentarius*—The Geotropism of *Fomes fomentarius* Fruit-bodies—The Attachment of *Fomes fomentarius* Fruit-bodies—The Spore-fall Period of *Fomes igniarius*—Winter Break in the Spore-fall Period of *Daedalea confragosa*—Solitary and Imbricated Fruit-bodies of Polyporeae, etc.

The Brief Spore-fall Period of Coprinus curtus.—In the first volume of this work [1] I pointed out that the period of spore-discharge for the fruit-bodies of certain Hymenomycetes was observed to be as follows: *Pleurotus ulmarius*, 17 days; *Polyporus squamosus*, *Polystictus versicolor*, and *Schizophyllum commune*, 16 days; *Lenzites betulina*, 10 days; *Psalliota campestris* and *Stereum hirsutum*, etc., a few days; and I also said that "smaller species of Coprinus, such as *C. plicatilis*, shed their spores in a few hours." In what follows I shall supplement this last statement with a series of exact observations made on *Coprinus curtus*, and I shall show that some of the smaller fruit-bodies of this fungus actually shed all their spores in the course of a few minutes.

Coprinus curtus is a small species which, although very common on horse dung both in England and Canada (Fig. 32), appears not to have been observed by Fries. It is described and illustrated in colour in Lange's revision of the genus Coprinus.[2] The Coprinus

[1] Vol. i, 1909, pp. 102–104.

[2] Jakob E. Lange, "Studies in the Agarics of Denmark," *Dansk Botanisk Arkiv udgivet af Dansk Botanisk Forenig*, Part II, No. 3, 1915, Plate I, Fig. *h*, also p. 45.

of which I described the geotropic swinging in Volume I, which I was unable to identify and therefore for convenience called *C. plicatiloides* (Vol. I, Figs. 26 and 27, pp. 70 and 72). is certainly

FIG. 32.—*Coprinus curtus* (= *C. plicatiloides* of Vol. I). Fruit-bodies on unsterilised horse dung in a large glass chamber in the laboratory at Winnipeg, at about 11 A.M. All (except one central very rudimentary one showing a speckled pileus only) belong to a single daily crop and all will have shed their spores and have begun to collapse by about 2 P.M. The largest pileus shows the characteristic reddish scales on its upper surface. As each pileus flattens out, its narrow disc becomes depressed like that of *Coprinus plicatilis*. Natural size.

C. curtus.[1] *Coprinus curtus* has a pileus which is foxy-red when very young and which, when expanded, bears a certain number of small scales which are composed of spherical cells and vary from a deep red colour to a watery white. Its spores are oval

[1] I have described *Coprinus curtus* minutely in "Three New British Coprini," *Trans. Brit. Myc. Soc.*, vol. vi, Part IV, 1920, pp. 364–365, and again in Volume III of this work.

and deep black, and it entirely lacks cystidia on the surface of its gills.

I procured the fruit-bodies of *Coprinus curtus* at will in winter-time by proceeding as follows. Frozen dung-balls were collected from the streets of Winnipeg and placed in a large glass vessel which was then covered with a glass plate and set on a table near a window in the laboratory. The dung-balls soon thawed. Usually, after from 10 to 14 days, a number of fruit-bodies of *Coprinus curtus* made their appearance on some, and often all, of the dung-balls; and, thereafter, for more than a week, a crop of fruit-bodies of this same species came to maturity daily. The dung-balls were sprayed or otherwise wetted as seemed necessary to keep the culture in good condition.

Several of the smaller Coprini show a distinct diurnal rhythm in the production of their fruit-bodies. Thus a form of *Coprinus ephemerus*, which commonly occurs on horse dung along with *C. curtus* at Winnipeg, only opens its pilei about midnight, and before 9 o'clock in the morning all its spores have long been shed. There are several other small species of Coprinus which behave like *C. ephemerus* and, if one desires to study the expansion of their pilei and the autodigestion of their gills, one must work through the night instead of through the day. *Coprinus curtus*, however, differs from these species in that it expands its diurnal crop of fruit-bodies not in the night but in the morning and early afternoon. It is on this account that I have chosen *C. curtus* as a fungus upon which I might make various observations, including those shortly to be recorded.[1]

The largest of the fruit-bodies which came up spontaneously on the horse dung used in my observations had a stipe which, when fully elongated, was 8 cm. high and a pileus which, when expanded and flattened, was 1·75 cm. wide. The smallest were veritable dwarfs. One of them, which was carefully measured, had a stipe only 6 mm. high and a pileus only 1·5 mm. in diameter. The other

[1] The rhythmic production of fruit-bodies by certain small Coprini, like the rhythmic production of asci in Ascobolus and of sporangia in Pilobolus, is undoubtedly due to the alternation of periods of light and darkness in every 24 hours; but exactly how and when the light influences these fruiting structures is at present unknown.

fruit-bodies in the culture ranged in size between these extremes. I observed the length of the spore-fall period in a number of fruit-bodies of different sizes, and the results of these observations are given in the Table below.

The method of observation was as follows. Fruit-bodies were chosen for study which happened to be coming up very close to the side of the closed glass vessel in which they were contained. These fruit-bodies, without their being disturbed in the slightest degree, were then observed from without from the time their conical pilei began to expand until all their spores were shed. The optical apparatus used for observing the fruit-bodies through the glass side of the container was sometimes a horizontal microscope (Pl. IV, Fig. 29, in Vol. I), sometimes a hand-held low-power objective of a microscope, and sometimes a pocket lens; and some large fruit-bodies were observed merely with the naked eye. Certain small fruit-bodies came up so near to the glass side of the container that with a low-power objective I was able to observe their black spores as they fell from the gills through the air; but with more distant fruit-bodies this could not be done. The spores are shed from the fruit-bodies of *Coprinus curtus* in the same manner as from those of larger Coprini such as *C. comatus* and *C. atramentarius*, *i.e.* in succession from below upwards on each gill or, as the pileus flattens, from the periphery of the pileus centripetally toward the stipe. Spore-discharge does not begin until the pileus has become almost plane. As soon as the spores begin to fall, a spore-free zone is created all around the periphery of the pileus. This zone, owing to the loss of its black spores, appears white when observed either with a lens or with the naked eye, and it gradually extends from the periphery of the pileus centripetally toward the stipe. As soon as it has covered the whole of the hymenium spore-discharge has ceased. The white spore-free zone on any pileus under observation began to be developed at a definite time and completed its development at a definite time. These times were carefully noted and the first was then subtracted from the last. The difference gave the spore-fall period. The following Table records the results of a series of observations made on seven fruit-bodies during the morning of February 3, 1914.

The Spore-fall Period of Coprinus curtus.

Fruit-body.	Diameter of the expanded Pileus.	Time of Day at which Spores fell.	Duration of the Spore-fall Period.
No. 1	15 mm.	11 A.M. to 1.25 P.M.	2 hours 25 minutes
No. 2	17·5 mm.	8.5 A.M. to 9.50 A.M.	1 hour 45 minutes
No. 3	12 mm. approx.	11 A.M. to 12.30 P.M.	1 hour 30 minutes
No. 4	10 mm.	10 A.M. to 11.15 A.M.	1 hour 15 minutes
No. 5	9 mm.	10.10 A.M. to 11.15 A.M.	1 hour 5 minutes
No. 6	4 mm.	9.10 A.M. to 9.45 A.M.	35 minutes
No. 7	2·5 mm.	10 A.M. to 10.30 A.M.	30 minutes

The data recorded in the Table show that the largest of the fruit-bodies observed shed their spores in less than 2·5 hours and the smallest in about 30 minutes. It is conceivable that some of the smallest dwarfs of this species, *i.e.* those having a pileus diameter of only 1·5 mm., shed their spores under favourable conditions in about 15 minutes.

The data recorded in the Table also show that, on the whole, the larger the fruit-body, the longer the spore-fall period. This, of course, is correlated with the fact that the zone of spore-discharge must traverse a greater radial distance in larger fruit-bodies than in smaller ones. All fruit-bodies are not equally vigorous, for I have sometimes noticed that, of two fruit-bodies having pilei of the same size and growing as near neighbours in the same culture, one opens its pileus and sheds its spores somewhat quicker than the other. The duration of the spore-fall period of any fruit-body is therefore affected not merely by the size of the pileus but also by its rate of development.

A single observation similar to those just recorded for *Coprinus curtus* was made on a small fruit-body of *Coprinus lagopus*. This fruit-body possessed a stipe which, when fully extended, was 27 mm. long and a pileus which, when fully expanded, was about 5 mm. in diameter. The duration of its spore-fall period was 1 hour 35 minutes. I have no doubt that the dwarf fruit-bodies of *Coprinus lagopus*, which were described in Chapter III and which have pilei from 1 to 3 mm. wide, are able to liberate all their spores in a few minutes just as do the smallest fruit-bodies of *C. curtus*.

Macroscopic Observations on the Fall of Spores of Armillaria mellea.—The emission of spore-clouds from certain Polyporeae growing under natural conditions has been observed macroscopically by various observers : by Hoffmann [1] from *Polyporus destructor* ; by Hermann von Schrenk [2] from *P. Schweinitzii* (Fig. 33) ; by myself [3]

Fig. 33.—*Polyporus Schweinitzii*, growing upon the stump of a *Pinus sylvestris*. H. von Schrenk, in the U.S.A., saw a fruit-body of this species emitting clouds of spores. Photographed by Somerville Hastings at Oxshott, Surrey, England. About $\frac{1}{3}$ natural size.

and Brooks [4] from *Polyporus squamosus* ; by Stone [5] from *Fomes pinicola* ; by Faull [6] and myself from *F. fomentarius* ; and by White [7]

[1] H. Hoffmann, *Jahrb. für wiss. Bot.*, Bd. II, 1860, p. 315.

[2] H. von Schrenk, "Some Diseases of New England Conifers," *Bull. 25, U.S. Dep. of Agric.*, 1900, p. 22.

[3] A. H. R. Buller, *vide* these *Researches*, vol. i, 1909, pp. 89–93. Since 1909, on three successive days, I saw dense spore-clouds passing away from a large *P. squamosus* fruit-body situated on the trunk of an Elm, about 10 feet from the ground, in the Priory Road at Kew.

[4] F. T. Brooks, "Notes on *Polyporus squamosus* Huds.," *The New Phytologist*, vol. viii, 1909, p. 350.

[5] R. E. Stone, "Visible Spore-Discharge in *Fomes pinicola*," *Trans. Brit. Myc. Soc.*, vol. vi, 1920, p. 294.

[6] *Vide infra.*

[7] J. H. White, "On the Biology of *Fomes applanatus*," *Trans. Roy. Can. Institute*, Toronto, 1919, p. 140.

and myself [1] from *F. applanatus*. Similarly, Banker [2] saw spore-clouds coming away from the under side of some large fruit-bodies of *Hydnum septentrionale*. Hitherto, however, no one appears to have perceived with the naked eye and under natural conditions the escape of the spores from beneath the pilei of any of the Agaricineae.[3] I shall therefore not hesitate to describe my own successful observations upon *Armillaria mellea*—the well-known Honey Fungus.

During the Worcester Foray of the British Mycological Society, held late in September, 1921, clusters of *Armillaria mellea* fruit-bodies were frequently found growing on the ground above stumps and buried roots. In one of the woods of Wyre Forest some fruit-bodies of this fungus were protected from the wind owing to the fact that they were half-covered with Brambles, were surrounded by tall Bracken-fern leaves, and grew in a spot that was enclosed by large Oak trees (Fig. 34). The result on still days was that, although many of the spores were doubtless carried away by slight air-currents, vast numbers of them settled in the immediate neighbourhood of the pilei, and thus whitened with a spore-deposit the upper surfaces of the adjacent Bramble leaves.

I had come to the theoretical conclusion that, since Agaricineae, like Polyporeae, shed vast quantities of spores, and since spore-discharge had been seen macroscopically in several large Polyporeae, under favourable conditions one ought to be able to observe with the naked eye the spore-stream passing out from beneath the pilei of large Agaricineae. All that remained was to put the theory to a practical test. The spore-deposits on the Bramble leaves shown in Fig. 34 suggested that *Armillaria mellea* would be a suitable lamellate species for the first trial. Shortly after leaving the fruit-bodies shown in Fig. 34, I found another cluster of Armillaria

[1] I saw spore-clouds coming away from beneath a large *Fomes applanatus* fruit-body in Kew Gardens during late August and early September, 1921. I was able to show the phenomenon to several observers.

[2] H. J. Banker, *vide infra*.

[3] Hammer ("A Note on the Discharge of Spores of *Pleurotus ostreatus*," *Torreya*, vol. v, 1905, p. 146) saw tiny wreaths of spores ascending to a height of 2–3 feet from a fruit-body of *Pleurotus ostreatus*, but the fruit-body had been gathered and placed on a table: it was not therefore under natural conditions.

fruit-bodies which was larger than the first (about a foot in diameter) and was situated in more open and much better lighted ground (Fig. 35). This seemed to offer all the facilities requisite for observation. I therefore threw myself at full length on the ground, brought my eyes to within a foot of the fruit-bodies and, in a horizontal direction and with a dark background, gazed intently at the air on the lee side of the cluster. Within a few seconds I

Fig. 34.—Natural spore-deposits of *Armillaria mellea*. Cluster of fruit-bodies on the ground in a wood, protected from wind by Bracken ferns, etc. Some of the escaping spores have settled upon, and have thereby whitened, the adjacent Bramble leaves. Photographed in Wyre Forest by Somerville Hastings. About $\frac{1}{8}$ natural size.

readily perceived the spores passing out between the fruit-bodies and escaping from the cluster in the form of a delicate cloud which, as it drifted away in the still air, resembled a fairy snow-storm or curls and wreaths of the finest tobacco smoke. This observation was at once verified by Mr. A. D. Cotton and Dr. Somerville Hastings who happened to be with me. Both these gentlemen assured me that they had no difficulty in seeing the spore-stream.

Banker's Observations on Spore-discharge in Hydnum septentrionale.—*Hydnum septentrionale* is a giant among the Hydneae and rivals in size the very largest of the Polyporeae. It was originally

described by Fries from a specimen found in Sweden ; and I myself have seen it at Winnipeg growing upon *Acer Negundo*, the Manitoba Maple (for illustrations, *vide infra*).[1] At Greencastle, Indiana, upon a living Beech tree, Banker found a mass of imbricated fruit-bodies of this species which was 30 cm. long and 45 cm. wide and which, after being damaged with the loss of a portion of its substance, weighed 35 lbs.[2]

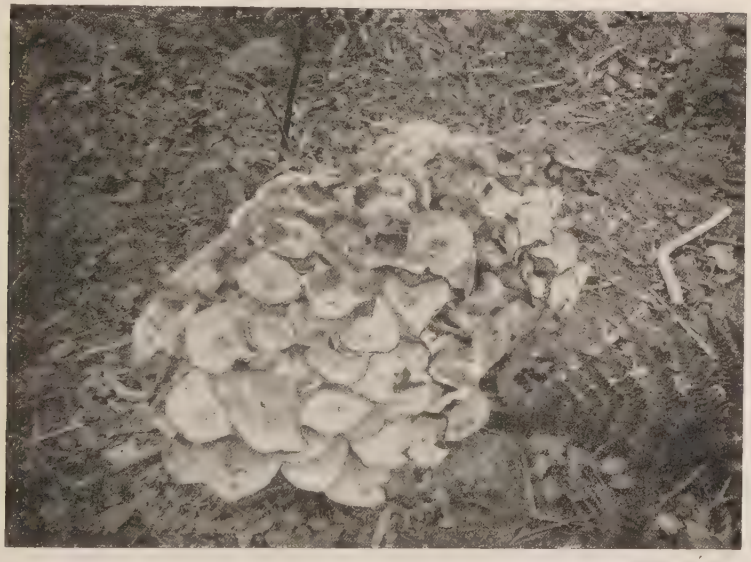


FIG. 35.—A cluster of *Armillaria mellea* fruit-bodies, of which the escaping spore-clouds were seen with the naked eye. The whiteness of the tops of the pilei and of the ground around the cluster was due chiefly to the presence of a thin spore-deposit formed by the settling of a certain number of the spores. Photographed in Wyre Forest by Somerville Hastings. About $\frac{1}{6}$ natural size.

Banker's remarks [3] concerning the spore-discharge of the fungus-mass just described are as follows. "The spores are produced in enormous numbers, but seemingly for only a few days. On my first visit to the plant, October 17, no spore-fall was observed, but the matter was not especially tested. Two days later, on visiting

[1] Chapter VI, Figs. 52, 53, and 54.

[2] H. J. Banker, "*Steccherinum septentrionale* (Fr.) Banker in Indiana," *Proc. Indiana Acad. of Sci.*, 1910, p. 213. I have estimated the width from Banker's photograph ; the length and weight are as given by him.

[3] *Ibid.*, p. 216.

the place, spores were observed rising from the mass in small clouds. These frequently streamed out from parts of the fungus like a puff of smoke for 10 or 15 seconds, then ceased and after two or three minutes began again. Such streams were emitted from different parts of the plant irregularly, so that from some part spores were escaping almost constantly. The day was pleasant and the air very quiet, yet occasionally a light puff of air passed over the plant. The streaming of the spores, however, appeared to be no more marked when the air stirred than when it was perfectly quiet."

Banker then says: "My own observation on *Steccherinum septentrionale* conforms to von Schrenk's description of the spore-discharge in *Polyporus Schweinitzii*. Buller accounts for the intermittent clouds by tiny irregular air currents, and thinks the spores were in reality 'falling continuously and regularly by their own weight.' In the case of his own observation on *Polyporus squamosus* this view appears to be confirmed, and he likens the appearance to the steam arising from a cup of tea in irregular eddies or the curling of tobacco smoke from the bowl of a pipe.[1] Had he observed the discharge in *Steccherinum septentrionale* I believe he would not have felt so confident of his explanation. The cloud-like discharge was more as the curling smoke of the tobacco when one breathes at intervals through the pipe. I doubt if the discharge is due to any propelling force as hinted by von Schrenk, but it seems to me probable that over certain restricted areas there is a simultaneous liberation of great quantities of spores followed by a period of rest. That such intermittent spore release occurs in all Hymenomycetes is improbable, but it seems to account for the phenomenon as observed in *Steccherinum septentrionale* and *Polyporus Schweinitzii*."

Banker's observations are interesting as being the first of their kind made upon any Hydnum, but his explanation of the irregular spore-clouds which he observed coming from the fruit-bodies I regard as probably erroneous. The supposition that over restricted areas of the fungus there was "a simultaneous liberation of spores followed by a period of rest" lacks experimental proof and is

[1] *Vide* these *Researches*, vol. i, 1909, pp. 89–90.

contrary to what I should expect (1) from my beam-of-light studies of spore-discharge in Polyporeae and Agaricineae, and (2) from my microscopic studies of the organisation of the hymenium in the Hymenomycetes generally. When a beam of light is directed beneath the pileus of any fruit-body liberating spores, one can see the spores as points of light with the naked eye; and then one can observe directly that the spore-stream coming from beneath the pileus is remarkably constant in density.[1] I have examined a large number of fruit-bodies in this way and can state that I have never once found an exception to this rule. Never have I found a fruit-body in which there was a rapid discharge of spores for a few seconds or a minute or two and then a pause of a few seconds or minutes before spore-discharge recommenced. I am strongly inclined to believe that if *Hydnum septentrionale* were to be tested by the beam-of-light method, it would be found to discharge its spores in the same regular manner as other Hymenomycetes. The slight irregular air-currents playing about such a large fungus-mass as Banker observed in the open are invisible to the naked eye and can only be revealed by the movements of the spores which, falling downwards very slowly by their own weight,[2] are passively carried away by them. One cannot predict how these tiny air-currents will move in respect to either speed or direction; and, in my judgment, it was only their irregularity and intermittency which gave the impression to Banker that spore-discharge from his *Hydnum septentrionale* was irregular and intermittent. Finally, I have studied microscopically the production and liberation of spores from certain Hydneae, although not from the species in question, and have come to the conclusion that they take place as in the Agaricineae where the basidia come to maturity in constant succession, discharge their spores as soon as they are ripe, and thus cause a certain number of spores to be liberated from every square millimetre of hymenial surface per minute.

The Vernal Spore-fall Period of Fomes fomentarius.—Mycologists have long been much puzzled how and when certain species of

[1] *Vide* these *Researches*, vol. i, 1909, p. 96.

[2] The rate of fall of spores of Hymenomycetes in still air varies according to their size and moisture contents. In many species it is only 1–2 mm. per second and sometimes less than 1 mm. *Vide* these *Researches*, vol. i, 1909, p. 175.

Fomes develop and liberate their spores. This puzzle, so far as the Tinder Fungus, *Fomes fomentarius*, is concerned (Figs. 36 and 37), has recently been solved by Dr. J. H. Faull of the University of Toronto. The late Professor G. F. Atkinson of Cornell University, whose knowledge of fleshy fungi was very great, told Dr. Faull a

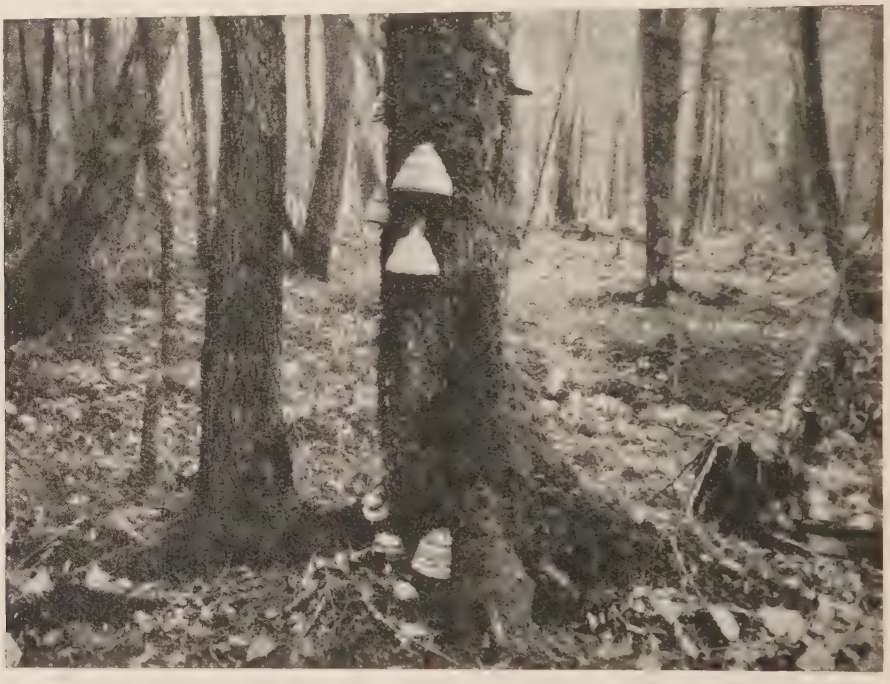


Fig. 36.—*Fomes fomentarius*. A number of fruit-bodies, each several years old, on a Yellow Birch trunk in a wood near Phillips, Wisconsin, U.S.A. Photographed by C. J. Humphrey of the Forestry Branch of the United States Department of Agriculture.

few years ago that he had never been able to discover any spores on the hymenium of *Fomes fomentarius*; and he laid a wager that Dr. Faull would be equally unsuccessful. Dr. Faull accepted this challenge and, thereafter, by systematic investigation, made the interesting discovery that *Fomes fomentarius develops each new layer of hymenial tubes in the autumn but delays the production and liberation of spores from these tubes until the spring*. Thus, between the autumnal development of a layer of tubes and the vernal development of the basidia and spores, there is a winter resting

period of several months' duration. It is now easy, therefore, to explain the failure of Atkinson and other mycologists to find the spores on the basidia of our Fomes : they all searched at the wrong season of the year ; they cut sections through the hymenial tubes in the autumn instead of in the spring.

Thanks to the kindness of Dr. Faull, I have been able to observe for myself that *Fomes fomentarius* does actually liberate its spores in the spring. In order to show me this phenomenon, Dr. Faull took me, on May 26, 1919, at Toronto, on an excursion into the little valley which is spanned by the new viaduct. There, upon a bank at the edge of a wood, were growing a number of ancient Birch-trees (*Betula lutea*) which were far past their prime ; and from the trunk of one of them, about 2 feet above the ground, projected several of the characteristically hoof-shaped fruit-bodies of *Fomes fomentarius*. These fruit-bodies each contained a series of annual layers of very fine hymenial tubes and, according to Dr. Faull, were about six years old. As we approached the tree-trunk, it became obvious that the fruit-bodies were producing and liberating their spores ; for a white spore-cloud, like fine smoke, was being given off beneath each one of them. This spore-cloud could be easily discerned at a distance of 10 feet and it was slowly being carried away by slight lateral currents of air. It thus exactly resembled the spore-cloud of *Polyporus squamosus* which I described in Volume I of this work.[1] We watched it for some minutes, but it grew neither thicker nor thinner except in so far as it was affected by slight changes in the speed of the air-currents. A number of spores had settled near-by on the bark of the tree and upon the tops of the fruit-bodies themselves, to which situation they had doubtless been carried by slight upward movements of the air during very still weather. The thickness of the white spore-deposit suggested that the liberation of spores from the fruit-bodies must have been going on for several previous days and nights.

In most Hymenomycetes, as soon as the gills, tubes, spines, etc., have come into existence, the associated hymenium immediately proceeds with its development, which only ceases after all the spores have been liberated. *Fomes fomentarius*, with its

[1] Vol. i, 1909, pp. 89–93.

autumnal development of tubes and its vernal production of spores, is a striking exception to this rule and in this respect differs from other well-known Fomes species, such as *F. applanatus* and *F. igniarius*. *F. applanatus* (*vide* Chap. V for illustrations) certainly has the normal mode of development, for I have observed that its fruit-bodies produce a new layer of tubes in the spring and summer and, when growing near the ground in secluded places, deposit beneath themselves a thin brown layer of spores in the late summer and early autumn (August and September). White's more detailed observations on the spore-discharge period of this fungus will be described and discussed in the next Chapter. We shall concern ourselves with the summer spore-discharge period of *F. igniarius* in another Section. It is not unlikely that some other species of Fomes resemble *F. fomentarius* in vernal spore-production; but, for the present, they await discovery.

Perennial Spore-production by One and the Same Tube-layer in Fomes fomentarius.—Another remarkable discovery made by Faull in his investigation of *Fomes fomentarius* is that in this species *each annual hymenial tube-layer may produce a crop of spores for four years in succession.*[1] Hitherto, it has been tacitly assumed that a layer of hymenial tubes in any species of Fomes functions for one year and for one year only; but now, so far as *Fomes fomentarius* is concerned, this old assumption has been found by Faull to be without justification. Let us suppose that in the spring of 1924 we have before us a fruit-body of *F. fomentarius* five years old, which produced annual tube-layers in the summers of 1920, 1921, 1922, and 1923. Then, assuming the correctness of Faull's observations, with the advent of the spore-discharge period, we should find that spores were being liberated not only from the tube-layer produced in 1923 but also from the tube-layers produced in 1922, 1921, and 1920. Moreover, if from 1920 to 1924 we could have investigated the tube-layer produced in the summer of 1920, we should have found that it would have produced and liberated spores not only in

[1] J. H. Faull, "Further Observations on the True Tinder Fungus," a paper communicated to a joint meeting of the Mycological Section of the American Bot. Soc. and the American Phytopath. Soc., held at Toronto, December, 1921, under the auspices of the American Ass. for the Adv. of Science. Cited from the abstract.

the spring of 1921, but also in the spring of the years 1922, 1923, and 1924. This is an entirely new conception of hymenial activity in the Polyporeae and affords further evidence of the high efficiency

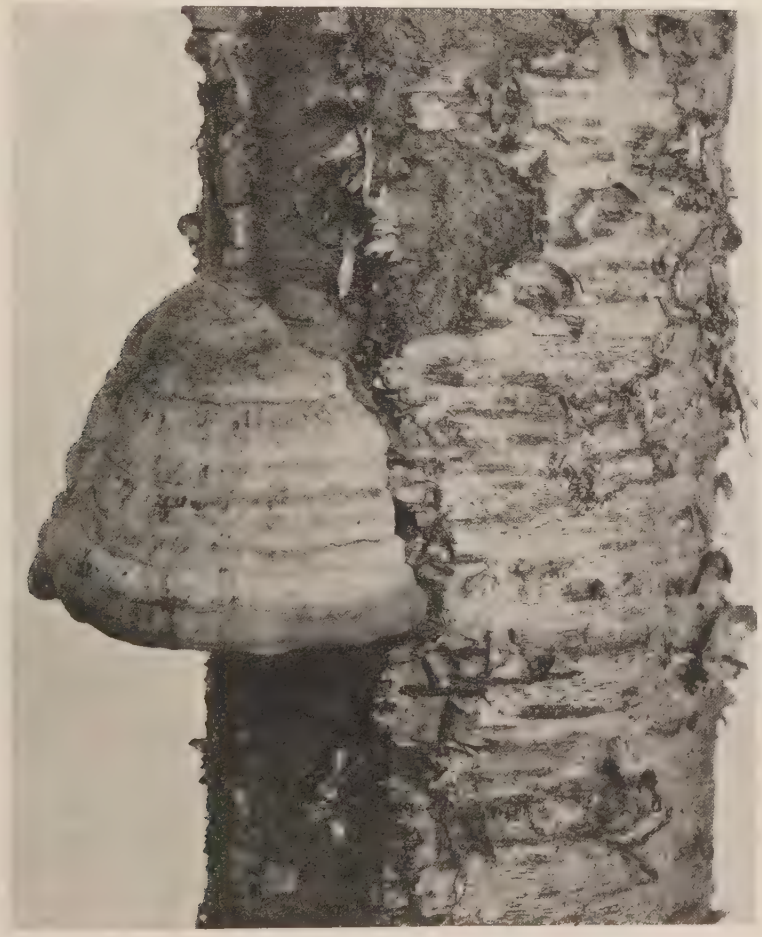


FIG. 37.—A fruit-body of *Fomes fomentarius*, probably six years old, attached to the trunk of a Birch, *Betula lutea*. Obtained in Algonkin Park, Ontario, Canada. Photographed by J. H. Faull. About ½ natural size.

of Fomes fruit-bodies as organs for the production and liberation of spores. It will be of interest to learn whether in a hymenial tube of a tube-layer which has functioned for four years four new hymenial layers are formed one above the other, thus slightly

narrowing the diameter of the tube, or whether the same hymenial layer functions each year by the pushing up into it of new basidia developed from the subhymenium.

The Geotropism of Fomes fomentarius Fruit-bodies.—There

Fig. 38.—*Fomes fomentarius.* The fruit-body was attached at *a* to the under side of a Birch branch and, reacting to the stimulus of gravity, grew conically downwards in the air for five years. During this time it produced the five successive annual hymenial tube-layers, 1–5. In the winter of the fifth year the tree was over-turned, so that the fruit-body took up the position here shown. The fruit-body then grew geotropically downwards at its edge, producing in the sixth and seventh years the tube-layers 6 and 7 respectively. From the shore of Indian Bay, Shoal Lake, Manitoba. Photographed by C. W. Lowe. Natural size.

can be no doubt that the stimulus of gravity plays a very important rôle in moulding the forms of Fomes fruit-bodies and in determining the direction of their growth. As an illustration of this fact, we may consider the curiously-shaped fruit-body of *Fomes fomentarius*, represented in Fig. 38, which was found by my colleague Mr. C. W. Lowe on a fallen Birch tree at Indian Bay, Shoal Lake, Manitoba, in July, 1921. The fruit-body had the orientation shown in the

photograph. It had started its development on the under side of a branch of a Birch and, in response to the stimulus of gravity, had grown vertically downwards for five years, so that during all this period it had a conical form and was hanging freely in the air from its point of attachment. It appears that in the winter of the fifth year the Birch tree was broken at its base with the result that the long axis of the fruit-body was turned upwards through an angle of about 135°, thus taking up the position shown in the photograph. Notwithstanding this displacement caused by the fall of the tree, the fruit-body continued to grow. In the sixth year it produced a hard crust over the mouths of the upwardly directed hymenial tubes and, at the same time, grew downwards at its lower edge so as to form a new horizontal layer of hymenial tubes ; and, in the seventh year, it produced another horizontal layer of tubes. Each new tube of the sixth and seventh years was as perfectly vertical as had been originally the tubes developed during the first five years.

A consideration of all the above facts justifies one in summing up the relations of a fruit-body of *Fomes fomentarius* to gravity as follows : (1) the fruit-body as a whole is positively geotropic, for its axis elongates in the direction of the earth's centre ; (2) the hymenial tubes are all positively geotropic, their response to the stimulus of gravity being very exact indeed ; (3) the sterile crust on the exterior of the fruit-body is plagiogeotropic, for it grows downwards at a definite angle with the vertical (it thus allows of an increase in the diameter of each successive annual layer of hymenial tubes) ; (4) each annual tube-layer, as a whole, is transversely geotropic, in consequence of which its under pored surface is remarkably horizontal ; and (5) the hard supporting and protective crust is formed on the upper side of the fruit-body rather than on the under side, and the naked open tubes which are relatively soft are formed on the under side of the fruit-body rather than on the upper side, as a result of the morphogenic stimulus of gravity.

The various responses of the fruit-bodies of *Fomes fomentarius* to the stimulus of gravity appear to be essential for permitting these organs to become efficient producers and liberators of spores. The most wonderful response of all seems to me to be the

extraordinarily exact downward growth of the hymenial tubes. Each tube grows downwards for 4–10 years and, according to Faull, as we have seen, the portion of a tube produced in any one year may function for as many as four successive years. If it were not for the fact that each of the exceedingly narrow and relatively very long hymenial tubes grows vertically downwards with marvellous precision, it would not be possible for the spores shot from the basidia to fall freely downwards in a tube's interior space; for the spores are adhesive, the air in each tube is perfectly still, each spore falls vertically downwards often for an inch or more within a tube, and, if a spore touches the side of a tube in its fall, it sticks to it. The successful emergence of the spores through the mouths of the hymenial tubes is strictly dependent on the axes of the tubes being perfectly vertical.

The Attachment of Fomes fomentarius Fruit-bodies.—The mycelium of *Fomes fomentarius* growing in a vertical Paper Birch trunk (*Betula alba* var. *papyrifera*), when about to form a fruit-body, bursts through the lenticels and cracks in the bark over an area no larger than the print made by the tip of a finger or thumb upon a sheet of polished glass (Fig. 39). The hyphae passing through this area and thus connecting the mycelium in the wood with the developing fruit-body thereafter conduct to the fruit-body all the materials required for its growth in successive years. As the fruit-body grows downwards by annual increments, it comes to press against the trunk (Fig. 37) and, where it touches the corky bark, it flattens out against it and becomes firmly adherent to it without its hyphae penetrating through it. The result is that it is not difficult to separate large *Fomes fomentarius* fruit-bodies from Birch trunks by sudden pressure with the hand; for, if one presses such a fruit-body violently, the outer paper-like sheet of cork (Birch bark) to which the fruit-body is adherent is loosened from the inner sheets and, at the same time, the strands of hyphae passing through the connecting area at the back of the top of the fruit-body snap across. One cannot separate a fruit-body of *Fomes igniarius* attached to an Oak tree in this way, for the bark of the Oak does not consist of thin paper-like sheets of pure cork but is mechanically very tough and resistant.

The Spore-fall Period of Fomes igniarius.—*Fomes igniarius* frequently attacks living deciduous trees in both Europe and North America. In Central Canada and the adjacent parts of the United States its fruit-bodies are frequently found on Poplars. At Winnipeg I have noticed them especially on *Populus tremuloides* Michx. where they project from the bark of the tree-trunk at the base of the stubs of lateral branches (Fig. 40). The fruit-bodies grow slowly but may attain an age of 20–30 years.

At my request my colleague, Dr. G. R. Bisby, investigated *Fomes igniarius* during the summer of 1921 with a view to determining when the fungus discharges

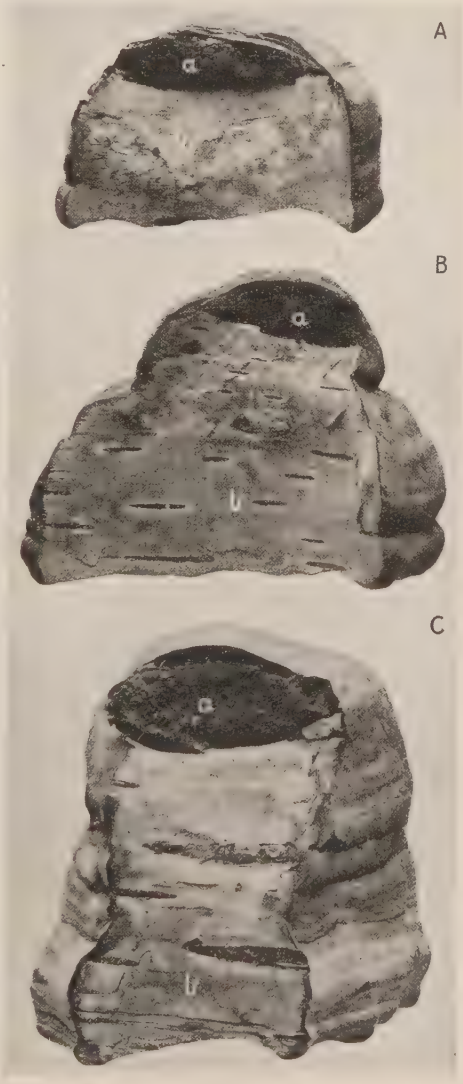


FIG. 39.—*Fomes fomentarius.* The backs of three fruit-bodies A, B, and C, one, two, and three years old respectively; to show the relation of a fruit-body with the mycelium in a Birch tree. The mycelium in each tree burst through the birch-bark only in the area *a*. The fruit-body began its development at *a* and then grew downwards, tending to take on a conical form but being prevented from doing so by the presence of the tree-trunk against which it came to press. It became so firmly adherent to the tree-trunk that when it was forcibly broken away therefrom, as shown at *b*, it carried with it a thin outer sheet of the birch-bark (cork), which is easily recognisable in B and C by the lenticels. However many years a fruit-body may continue its growth, its connection with the mycelium in the tree-trunk is only *via* the hyphae in the small area *a*. Fruit-bodies collected near the Lake of the Woods, Central Canada. $\frac{2}{3}$ natural size.

its spores ; and the following statements are taken from the notes that he kindly sent to me.

The pilei observed were projecting from the trunks of *Populus tremuloides* in the woods along the Red River at Winnipeg. Microscope slides were placed on a platform just below each of two pilei for the purpose of catching the spores immediately after their discharge, and they were examined at frequent intervals to determine the beginning of the spore-discharge period.

The slides were first put out on April 15, 1921. The hymenial tubes of the 1920 tube-layer were open ; but neither at that time nor subsequently did they discharge any spores.[1]

On May 27, the centre of the fruit-bodies showed a dark brown coating of the new hyphae which were to produce the new tube layer. By June 21, signs of the production of pore openings in the new growth were evident, but up to that time no spores had been discharged. The slides could not be examined again until July 17, at which time spores were being discharged in great numbers. Thus the exact date at which the phenomenon of spore-discharge began in 1921 was unfortunately not determined ; but it must have been between June 21 and July 17. Probably it was about July 1.

The discharge of spores continued from the beginning of the spore-discharge period (about July 1) until the beginning of September. On the first day of September very few spores were being liberated. The two fruit-bodies observed therefore had a spore-discharge period in 1921 of about two months' duration.

On some days during the spore-discharge period the discharge of spores was much heavier than on others. It was less on cooler days and, during a cool rainy period, very few spores were liberated.

Tests during 24 hours, August 11–12, showed that about the same number of spores was discharged during the 12-hour day period (9 A.M. to 8.30 P.M.) as during the 12-hour night period

[1] Possibly in *Fomes igniarius*, as in *F. fomentarius*, the tubes produced in any one year are active for several years. The 1920 tubes may have produced spores along with the 1921 tubes after the beginning of the spore-discharge period. This matter requires further investigation. I observed continuity of the tubes in successive tube-layers of some small fruit-bodies of the allied *F. pomaceus* gathered from a Plum tree at Banbury, England.

(8.30 P.M. to 8.30 A.M.). Evidently here, as in other Polyporeae

FIG. 40.—*Fomes igniarius* on a trunk of *Populus tremuloides*. Three fruit-bodies, each several years old, formed where lateral branches broke away and left stubs. Photographed by C. J. Humphrey in the State of Wisconsin. Courtesy of the United States Department of Agriculture. About ¼ natural size.

and the Hymenomycetes generally, the production and liberation of spores from mature fruit-bodies is not affected by light.

The number of spores produced per annum is probably much less from a fruit-body of *Fomes igniarius* than from fruit-bodies of *F. applanatus* and *F. fomentarius*, owing to the fact that the annual tube-layers in this species are very shallow. A rough count of the spores deposited on a slide during a 24-hour period, August 2–3, gave a total of about 83,000 spores per square mm.[1] The medium-sized fruit-body which produced the spores from which this count was made was about 32 square cm. in area. With favourable conditions for spore-discharge, therefore, it probably liberated about 260,000,000 spores in 24 hours. There are about 1,800 hymenial tubes per square centimetre of each tube-layer. Each tube, therefore, may liberate about 4,600 spores per day.[2]

On some days the discharge of spores is much lighter than that just indicated. Thus during 23 hours, August 7–8, only one spore on the average was produced per 300 square microns of slide area, or some 3,000 spores per square mm. This is only about one twenty-eighth of the number of spores (83,000) produced per square mm. during a similar period on August 2–3.

Summarising, we may say that Dr. Bisby's investigation indicates that for *Fomes igniarius* in Manitoba the usual course of events connected with the annual spore-discharge period is as follows: (1) the production of a new annual tube-layer during the first part of the summer, leading to (2) the discharge of spores for about two months (July, August, and the beginning of September), followed by (3) a period of quiescence during the late autumn, winter, and spring. Thus *Fomes igniarius* stands in marked contrast with *F. fomentarius* which produces a new annual tube-layer in the autumn and liberates spores from them in the spring.

Winter Break in the Spore-fall Period of Daedalea confragosa. In Manitoba the winter often sets in early in November, with the result that certain hymenomycetous fruit-bodies which grow on logs, sticks, etc., have their spore-discharge period

[1] About 100 spores per 1,200 square μ of slide in an average deposit, the deposit being one or two layers deep and practically covering portions of the slide.

[2] Apparently not all portions of the pileus gave off spores simultaneously; but this irregularity requires further investigation.

interrupted by the cold weather. Among species liable to suffer interruption in this manner one may mention: *Schizophyllum commune*, *Panus stypticus*, and species of Lentinus and Polystictus. Recently I obtained evidence of winter interruption of the spore-discharge period for *Daedalea confragosa*.

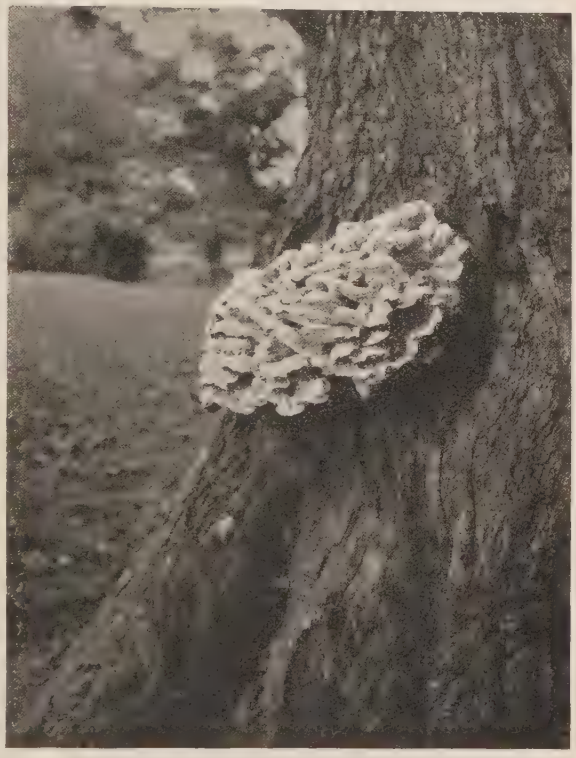


Fig. 41.—*Polyporus sulphureus*. A cluster of imbricated fruit-bodies growing on the dead wood of a living Oak in Sutton Park, Warwickshire. Photographed by J. E. Titley. About $\frac{1}{10}$ natural size. The cluster was 15 inches wide and 10 inches deep.

On April 23, 1922, shortly after the end of the winter and the disappearance of the snow, I found in a wood near Winnipeg several large fruit-bodies of *Daedalea confragosa* on a fallen tree-trunk. It was evident from their appearance that they had been developed in the autumn of 1921; and, as they were full-grown, there could be no doubt that they had shed an abundance of spores before the winter had arrived. I gathered the fruit-bodies, took them to the laboratory, moistened their upper surfaces, and put them in a large covered glass dish. During the next two or three days they formed thick white spore-deposits under their pilei, thus proving conclusively that they were still alive and had resumed the function of producing and liberating spores which had been interrupted by the winter's long frost.

Solitary and Imbricated Fruit-bodies of Polyporeae, etc.—The fruit-bodies of *Fomes officinalis* (Figs. 45, 46, and 47, Chap. V), *F. fomentarius* (Figs. 36, 37, pp. 106, 109), *F. igniarius* (Fig. 40, p. 115), *F. applanatus* (Figs. 43 and 50, Chap. V), *Polyporus hispidus*, and *P. betulinus*, are usually solitary. This solitariness appears to be correlated with the large size of the fruit-bodies in question and the downward elongation of their tube-layers. If, in such species, a number of fruit-bodies were to originate in a closely imbricated manner, one above the other, the hymenial tubes of one fruit-body, in growing toward the earth's centre, would, in the course of time, come into contact with the top of a subjacent fruit-body and thus have their apertures closed. As an accident, this sometimes actually happens with *Fomes applanatus* where two fruit-bodies have arisen too near together, one above the other. In *Polyporus squamosus*, fruit-bodies of very large size are often solitary (Fig. 1, Vol. I, p. 8). Not infrequently, however, in this species, several more or less imbricating fruit-bodies are produced in a cluster. Under such conditions they are sometimes too closely packed together, with the result that some of the spores have little or no chance of being carried off by the wind and, in consequence, are deposited as a white spore-deposit on the tops of pilei below the hymenial tubes concerned. On the other hand, in part owing to its solitariness, the large fruit-body of *Fomes officinalis* shown in Fig. 45 (Chap. V) grew downwards in the course of forty-five years for a distance of 2 feet and, during all that time, was perfectly free to liberate the spores from each annual tube-layer. The chances of a large fruit-body of a tree-trunk-inhabiting Polyporus or Fomes having all its spores carried away by the wind are certainly greatest when the fruit-body stands alone, and it is therefore interesting to note the general tendency toward solitariness exhibited by large fruit-bodies in these genera.

The fleshy, sulphur-yellow, annual fruit-bodies of *Polyporus sulphureus*, so often seen in Europe upon old Oak trees, Willows, etc. (Fig. 41), are, as a rule, considerably imbricated. This imbrication seems to be correlated with the relatively small size of each fruit-body and the shallowness of the layer of hymenial tubes.

The fungus, so to speak, has solved the problem of spore-production

FIG. 42.—*Polyporus radiatus*, a polypore which produces many small imbricating fruit-bodies rather than one large solitary fruit-body. Here the fruit-bodies are projecting from an Alder (Alnus) tree. Photographed by A. E. Peck in Yorkshire. About ¼ natural size.

by spreading out its hymenium in shallow tubes attached to a large number of small imbricating fruit-bodies rather than, as in

Polyporus hispidus, *Fomes applanatus*, etc., by spreading out its hymenium in deep tubes attached to a single very large fruit-body. The dispersal of the hymenium on many closely placed small pilei, rather than its concentration upon one very large pileus, is also to be observed in the bulky fruit-body masses of *Hydnum septentrionale* and in *Polystictus versicolor*, *Polyporus radiatus* (Fig. 42), *P. adustus*, *Stereum hirsutum*, etc. In the four last-named species the fruit-bodies are rarely, if ever, solitary; and often a score or more of them cover an extensive area on the side of an old tree-trunk or a stump. The pilei individually are small; but this finds a compensation in their large number.

Certain Polypori, *e.g. Polyporus giganteus*, *P. umbellatus*, *P. frondosus*, of which illustrations will be provided in Volume IV, have branched or compound fruit-bodies, one central stipe bearing many pilei. The compound condition of these fruit-bodies seems to be correlated with the fact that the species in question are terrestrial. The stipe grows upwards from the ground, branches and rebranches, a large number of small more or less imbricating fruit-bodies thus coming to be produced in the end about a central supporting axis. As in *Polyporus sulphureus*, these fungi, so to speak, have solved the problem of spore-production by spreading out their hymenium in shallow tubes attached to a large number of small imbricating pilei instead of by concentrating it in deep tubes attached to one very large pileus. The production of one central branching stipe bearing many pilei, instead of many stipes each bearing one pileus, effects a saving in fruit-body material and in the energy required for penetration through the soil.

CHAPTER V

FOMES APPLANATUS AND ITS SPORE-DISCHARGE PERIOD

Habitat and Hosts—A Wound Parasite—Spore Structure—The Longevity of the Fruit-body—The Longevity of Various Polyporeae—The Hymenial Tubes—The Spore-discharge Period—A Comparison of the Spore-fall Period of Certain Hymenomycetes—The Mechanical Consistence of Coprinus and Fomes Fruit-bodies Contrasted—The Number of Spores in *Fomes applanatus* and Other Basidiomycetes—The Cause of the Long Spore-discharge Period in *Fomes applanatus*—The Progressive Exhaustion of the Hymenial Tubes—The Significance of the Production of Vast Numbers of Spores

Habitat and Hosts.—The fruit-bodies of *Fomes applanatus* have been found upon upwards of fifty species of trees included in the following genera: (Dicotyledones) Acer, Aesculus, Alnus, Betula (Fig. 43), Carpinus, Crataegus, Fagus, Fraxinus, Gleditschia, Hicoria, Liriodendron, Malus, Morus, Nyssa, Populus, Prunus, Pyrus, Quercus, Robinia, Salix, Tilia, Ulmus, and Umbilicaria; (Coniferae) Abies, Picea, Pinus, Pseudotsuga, and Tsuga.[1] The fungus causes the decay of very large quantities of wood annually and must be considered as one of the most destructive of wood-destroying agencies.

A Wound Parasite.—J. H. White has recently shown that *Fomes applanatus*, when growing on living trees, is not a saprophyte, but is a wound parasite, *i.e.* a fungus which invades a tree *via* some exposed wound and which then progressively enters, kills, and destroys the living tissues of its host. His proof of parasitism is based on three arguments, the second of which appears to be not only novel but also conclusive. These arguments are as follows.

[1] G. G. Hedgcock, "Notes on Some Diseases of Trees in our National Forests," *Phytopathology*, vol. ii, 1912, p. 75; also vol. iv, 1914, p. 185. Also J. H. White, "On the Biology of *Fomes applanatus*," *Trans. Roy. Canadian Institute, Toronto*, 1919, p. 136. Hedgcock records 53 species attacked by the Fomes, and White 21.

(1) The mycelium works upwards in a tree-trunk most readily by way of the heart-wood, causing a characteristic decay, and outwards by way of the sap-wood, eventually reaching the cambium. Apparently, the mycelium causes the death of all the living tissues traversed. (2) A broad brown band is present in the wood of living trees along the advance line of the invading mycelium. Within

Fig. 43.—*Fomes applanatus*. A large fruit-body on a Yellow Birch trunk in a wood near Phillips, Wisconsin, U.S.A. Photographed by C. J. Humphrey of the Forestry Branch of the United States Department of Agriculture.

this band there is a copious production of wound-gum and an excessive multiplication of tyloses. This band steadily moves forward with the advancing hyphae, the tyloses and wound-gum being destroyed by the mycelium along its posterior margin as rapidly as they are formed along its anterior margin. The new production of the tyloses resulting from the advance of the mycelium shows that the invaded tissues of the host are living, while the subsequent destruction of the tyloses shows that the mycelium is parasitic. (3) Inoculation with the spores and mycelium of *Fomes*

applanatus into living trees results in an extensive browning of the inoculated wood with a multiplication of tyloses, the browning of the wood and the multiplication of the tyloses being far in excess of what is caused by traumatic stimulation.[1]

Spore Structure.—According to White, *Fomes applanatus* produces basidiospores only. These spores alone, therefore, bring about the dissemination of the fungus in nature. Conidia are not produced by the mycelium nor, as has commonly been affirmed, by the upper surface layer of the sporophore.[2]

The basidiospore-wall, according to White, is not simple but double, for it consists of an outer thin hyaline layer and an inner thick yellow papillate layer. White regards the whole spore as a thick-walled chlamydospore formed inside the thin exterior hyaline wall.[3] I have examined the spores of *Fomes applanatus*, as well as the similar but larger spores of *Ganoderma colossus*, with the result that my conception of the spore-wall is quite different from that of White. It seems to me that each spore has one continuous, rather thick wall made up of two layers: (1) an outer, very thin, colourless, homogeneous layer formed whilst the spore is growing from a tiny rudiment to full size, and (2) an inner and much thicker layer, formed more slowly during the ripening of the spore, of a whitish or yellowish colour, and marked from within outwards by numerous fine yellowish-brown striae. What the nature of these striae is I do not know, but I do not regard them as papillae. Atkinson,[4] who first studied them and whose general conception of the wall is similar to my own, looks upon them as "perforations into which it appears that the brown or yellowish-brown contents of the spore project." The continuity of the two layers of the wall is shown by the fact that, if one takes dried spores of *Fomes applanatus* or *Ganoderma colossus* and places them in glycerine, no trace of air enclosed between the outer and inner wall-layers can be observed. In having a thin, colourless, outer wall-layer and a thick, pigmented, inner wall-layer the basidiospore of *Fomes*

[1] J. H. White, "On the Biology of *Fomes applanatus*," *Trans. Roy. Canadian Institute, Toronto*, 1919, pp. 159–167.

[2] *Ibid.*, p. 137.

[3] *Ibid.*, pp. 138, 167.

[4] G. F. Atkinson, "On the Identity of Polyporus 'applanatus' of Europe and North America," *Annales Mycologici*, vol. 6, 1908, pp. 179–191.

applanatus or *Ganoderma colossus* is strictly comparable with the basidiospore of many chromosporous Agaricineae, *e.g. Coprinus*

Fig. 44.—*Fomes applanatus.* A, upper surface of a large fruit-body three years old (same fruit-body as that shown in Fig. 48): *w*, wood of a Sycamore tree (*Acer pseudoplatanus*); *c*, centre of origin of fruit-body; the numbers 1, 2, and 3 show the limits of growth in the first, second, and third years respectively. B, a fruit-body resting on a block of Spruce wood, two years old, seen from below, showing the white under surface of the hymenial tube-layer. The pores are so minute that they cannot be distinguished. C, a vertical section through a piece of pileus-flesh and six successive annual tube-layers, the last in an early stage of development. Collected in Bavaria and photographed at the Forst-botanisches Institut, Munich, by Robert Hartig and the author. $\frac{1}{3}$ natural size.

stercorarius and *C. sterquilinus*.[1] As I see no reason for regarding the spores of Coprini, Panaeoli, etc., as involving chlamydospore

[1] *Cf.* Chap. II, p. 52.

formation, I think it best not to speak of chlamydospore formation in *Fomes applanatus*.

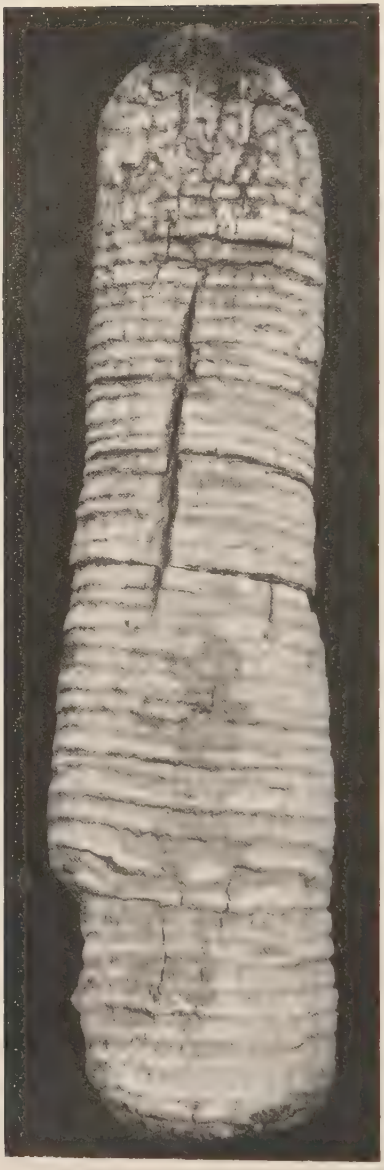
Atkinson's statement[1] that what had been regarded as "the truncate base" of a spore of *F. applanatus* is in reality the apex has been confirmed by White's studies of the attachment of the spores to their sterigmata in the living hymenium.[2] I have repeated White's observations and found them to be correct. The spores of *Fomes applanatus*, in being attached laterally by their pointed ends to the sterigmata and in being, when ripe and dry, more or less truncate at their distal ends, resemble the thick-walled spores of certain Coprini and other chromosporous Agaricineae. The distal end of the spore contains a germ-pore and is weaker than the rest of the wall. Hence it collapses as the spore dries, and becomes truncate.[3] The germ-tube always emerges through the germ-pore,[4] as during germination of the spores of Coprini.

The Longevity of the Fruit-body.—The fruit-body of *Fomes applanatus* produces a new layer of tubes each year of its existence (Fig. 44). In the spring, before a new layer of tubes is formed, a thin brown tough horizontal layer of flesh or context is formed by the ends of the old tubes, and from this the new tubes arise (*cf.* Fig. 48). The new layer of flesh completely closes the ends of the old layer of tubes above it, so that it is impossible for any layer of tubes to function for more than one year. The average length of life of a fruit-body, as determined by the number of its annual tube-layers, is 4 or 5 years and its maximum length of life from 8 to 10 years.[5] I found a large fruit-body near Montreal which protruded 9 inches from the stump on which it was situated and possessed seven deep annual layers of tubes which, even in their dried and shrunken condition, had a total depth of 4 inches.

The Longevity of Various Polyporeae.—Some other species of Fomes, *e.g. Fomes igniarius* and *F. officinalis*, certainly often greatly exceed *Fomes applanatus* in longevity.

I have in my possession a fruit-body of *Fomes igniarius*, given to me by Robert Hartig at Munich, in which 25 layers of tubes

[1] G. F. Atkinson, *loc. cit.*
[2] J. H. White, *loc. cit.*, p. 138.
[3] *Ibid.*, p. 138.
[4] *Ibid.*, p. 144.
[5] J. H. White, *loc. cit.*, p. 139.



can be counted; von Schrenk and Spaulding[1] found fruit-bodies of this same species with 50 layers of tubes; and Atkinson mentions a *Fomes igniarius* fruit-body which he found on a Birch in the Adirondacks, which had 80 layers of tubes.[2] Whether or not each layer of tubes in a fruit-body of *Fomes igniarius* represents the whole of one year's growth remains, however, to be determined by direct observation; but, in any case, I do not doubt that *Fomes igniarius* is much longer lived than *Fomes applanatus*.

Dr. Faull has kindly shown me a remarkable fruit-body of *Fomes officinalis*.[3] It was found at Ravelstoke, British Columbia, hanging from the inclined trunk of a Pine tree (*Pinus monticola*); it is cylindrical in form and has a length of almost exactly 2 feet

FIG. 45.—*Fomes officinalis*. A large cylindrical fruit-body, 1 foot 11·5 inches long, 7·5 lbs. in weight, gathered by Dr. R. Cameron at Ravelstoke, British Columbia, Canada, from a trunk of *Pinus monticola*, now in the possession of Professor J. H. Faull. It was attached to the tree by its top and was slightly flattened against the trunk on the opposite side to that in view. It has 45 annual rings of hymenial tubes. Photographed by J. H. Faull at the University of Toronto.

[1] H. von Schrenk and P. Spaulding, "Diseases of Deciduous Forest Trees," *Bur. of Plant Industry, U.S. Dept. of Agriculture, Bull.* No. 149, p. 29.

[2] G. F. Atkinson, *Mushrooms, Edible and Poisonous*, New York, 1911, p. 194.

[3] *Fomes officinalis* is the original *agaricum* of the ancient Greeks and Romans and has been of importance in medicine as a purgative from the time of Dioscorides

(Fig. 45). The number of its rings is 45. The average thickness of its rings therefore just exceeds one-half of an inch. In this fungus, owing to the distinctness of the rings on their exterior and owing to their great depth, I do not doubt that each ring represents the whole of the growth of the fruit-body for the year in which it was formed.

When the 45-year-old fruit-body just described was only six years old, it must have had only six annual tube-rings and must have resembled in form the 6-year-old fruit-body shown in Fig. 46 ; and, when it was fifteen years old, it must have had fifteen annual tube-rings and must have resembled in general form the less evenly grown 15-year-old fruit-body shown in Fig. 47.

The maximum age for certain species of Polyporeae, so far as

onwards. *Vide* A. H. R. Buller, "The Fungus Lore of the Greeks and Romans," a presidential address, *Trans. Brit. Myc. Soc.*, vol. v, 1914, pp. 58–60.

J. H. Faull has given us an interesting account of the fungus ("*Fomes officinalis*, a Timber-destroying Fungus," *Trans. Roy. Canadian Institute, Toronto*, vol. xi, 1916, pp. 185–209, Figs. 1–30) in which he makes the following statements. A fruit-body has the odour of fresh meal and an extremely bitter quinine-like taste. Long before the recognition of *F. officinalis* by botanists in America, the fruit-bodies were used by the early settlers in Ontario and Quebec for various purposes, including the preparation of yeast for bread-making, and the plant was known to them as the *Pineapple Fungus* (*Pineapple tree*, an obsolete English name for a pine or coniferous tree ; *pineapple* originally meant a pine cone). The first scientific record of the fungus in America appears to have been not earlier than 1886. There is some evidence that the Indians knew of its medicinal value. The active principle is a resinous substance *agaricin* ; and this, with other resins, constitutes up to 70 per cent. of the dry weight of the fruit-body. The resins are secreted in the form of amorphous granules to a very slight extent on the mycelium, but in great abundance on the hyphae of the sporophore. Quélet and certain other European systematists have assumed that *F. officinalis* is a variety of *Polyporus sulphureus* or specifically very close to it. However, these two species are very distinct, differing in : (1) size and branching of hyphae, (2) form, longevity, and content of sporophore, (3) structure of sporophore, (4) size of spores, and (5) cultural characters. *F. officinalis* causes a red heart-rot of conifers characterised by a removal of the cellulose, a fracturing of the wood into rectangular masses, and the formation of mycelial sheets in the crevices. Histologically the effects are similar to those caused by *P. Schweinitzii*. It occurs on living and dead timber and is a wound parasite. In Canada it has been found in Quebec, Ontario, and British Columbia ; and in the United States in Arizona, California, Oregon, Washington, Montana, Nevada, Idaho, Wisconsin, Michigan, and Wyoming. In Europe it occurs on *Larix europaea* and *L. sibirica* ; and in North America on *Abies concolor, A. magnifica, A. grandis, Larix occidentalis, L. laricina, Picea Engelmanni, P. sitchensis, Pinus lambertiana, P. murrayana, P. ponderosa, P. Jeffreyi, P. strobus, P. monticola, Pseudotsuga taxifolia, Tsuga heterophylla*, and *T. mertensiana*.

it has been ascertained by counting the successive tube-layers, is summarised in the following Table.

Age of Oldest Known Fruit-bodies of Certain Polyporeae.

Species.	Age in Years.	Observer.
Polystictus versicolor .	1	E. Fries, etc.
Polyporus squamosus .	1	E. Fries, etc.
Fomes applanatus . .	10	J. H. White
Fomes officinalis . .	45	J. H. Faull
Fomes igniarius . .	80	G. F. Atkinson

The Hymenial Tubes.—The fruit-body of *Fomes applanatus* is bracket-shaped and broadly attached to its woody substratum. Its broad attachment and its remarkably hard upper crust serve to keep the hymenial tubes fixed permanently in one position. The hymenial tubes are very long and yet extremely narrow. In one large fruit-body, in one layer, I found them to be 12 mm. long, except toward the margin of the pileus where they became progressively shorter, but they were only 0·17 mm. in internal diameter. In another very large three-year-old fruit-body (Fig. 48, p. 131), where the internal diameter of the tubes was also 0·17 mm., the length of the tubes (except near the margin of the pileus) varied in the first tube-layer from 9 to 12 mm., in the second from 19 to 28 mm., and in the third from 18 to 20 mm. In large well-grown fruit-bodies, therefore, the majority of the hymenial tubes vary in length from about 10 to 20 mm. and exceptionally attain a length of 28 mm., while their average internal diameter is only about 0·17 mm. From these data it can be calculated that the ratio of tube-length to tube-breadth in large fruit-bodies varies from about 60 to 120 and, exceptionally, is as great as 170. Now, as the hymenial tubes are relatively so very long and yet so very narrow, it is of high importance for the escape of the adhesive spores that the cylindrical lumen of each tube shall have its axis perfectly vertical; for the least deviation from this direction, *i.e.* a deviation of 1° or even less, will cause the spores shot from the basidia in the upper and middle parts of each tube into the intratubular cavity to strike the sides of the tube during their fall and to adhere there

(Fig. 49). The mode of attachment and the mechanical rigidity of the fruit-body as a whole are therefore important factors in bringing about the successful liberation of the spores.[1]

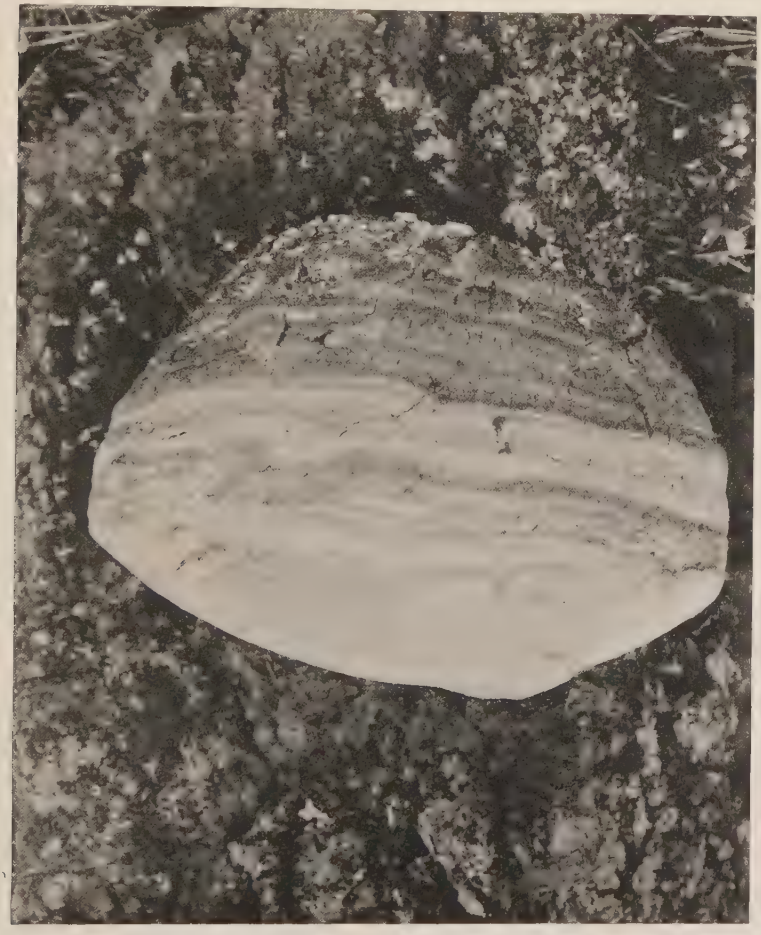


FIG. 46.—*Fomes officinalis.* A fruit-body with 5–6 layers of hymenial tubes, and therefore 5–6 years old, growing upon the trunk of *Pseudotsuga taxifolia* in Montana. Photograph supplied by G. G. Hedgcock of the U.S.A. Department of Agriculture. About ½ natural size. The width of the fruit-body was 7 inches.

The hymenial tubes are not only often upwards of 1 cm. in length and less than 0·2 mm. in diameter, *i.e.* very long and narrow,

[1] *Cf.* vol. i, 1909, pp. 39–40.

but also closely crowded (Fig. 48). In one fruit-body which I investigated, there were 2,080 tubes in 1 square cm. of a tube-layer. Since each tube is lined with a hymenial layer from top to bottom, other things being equal it follows that the longer and narrower the tubes, and the more the tubes are crowded together, the more spores can be produced by the tubes above any given area of the pored surface. As recorded in Volume I, the inner surface of the tubes of a single layer of tubes in one fruit-body was found to be 148 times as great as the flat under surface of the flesh to which the tubes were attached, so that the specific increase of the hymenial surface of the fruit-body due to the presence of a single layer of tubes was 148. Taking three years together the specific increase was 493.[1] Owing to the high specific increase of hymenial surface it can be no matter for surprise that, as White has directly observed, *Fomes applanatus* produces an almost incredible number of spores. White, using the methods I employed for *Polyporus squamosus*, found that a fruit-body of *Fomes applanatus* having a pored area of about 1 square foot liberated 30,000,000,000 spores in 24 hours.[2]

FIG. 47.—*Fomes officinalis*. A fruit-body with 15 annual layers of hymenial tubes, and therefore 15 years old; length 1 foot, breadth and depth each 7·5 inches, weight 5 lbs. Collected at Algonkin Park, Canada. Photographed by J. H. Faull. About $\frac{1}{5}$ natural size.

One square foot equals 930 sq. cm. Reckoning 2,080 tubes to 1 sq. cm., the number of tubes on the under side of White's

[1] Vol. i, pp. 32–33. *Fomes vegetus* is merely a synonym for *F. applanatus*.
[2] J. H. White, *loc. cit.*, p. 140.

fruit-body must have been approximately 930 × 2,080 or about 2,000,000. Since from these 2,000,000 tubes 30,000,000,000 spores were liberated in 24 hours, the average rate of emission of spores from each tube must have been about 15,000 per day of 24 hours, or about ten per minute, or about one every six seconds.

The Spore-discharge Period.—White has discovered that *Fomes applanatus* has a spore-discharge period which continues day and night uninterruptedly not for a few days only or even for a

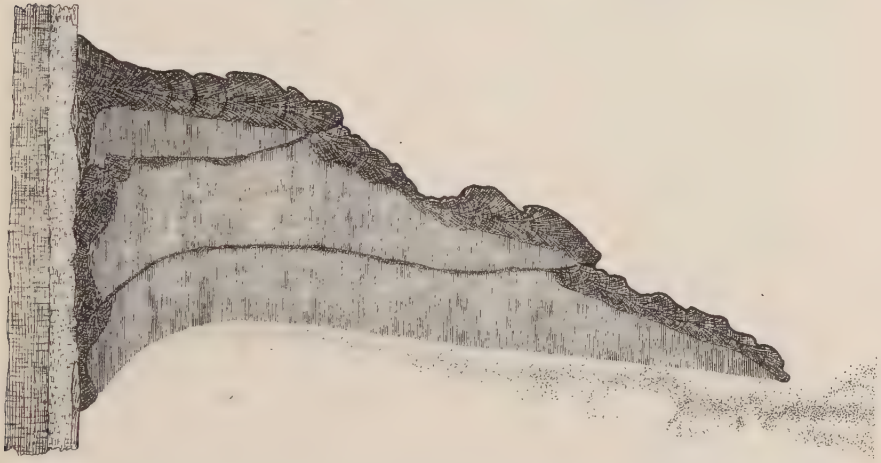
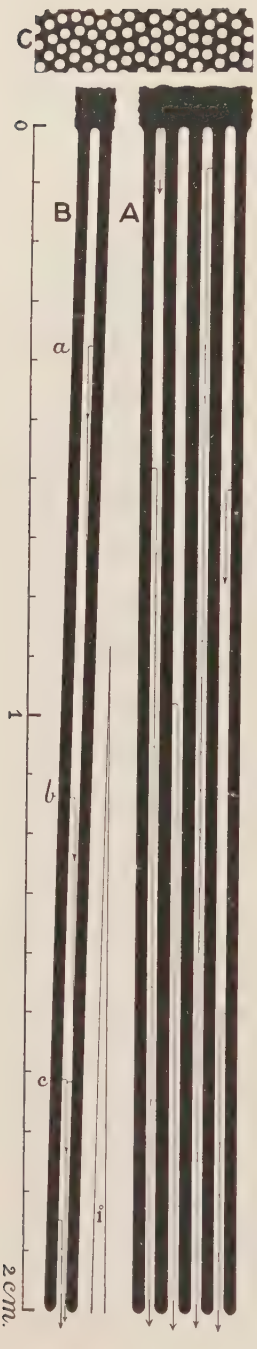


FIG. 48.—*Fomes applanatus*, a species with an annual spore-fall period of about six months' duration. Vertical section through a fruit-body three years old. The lowest and last-formed hymenial tube-layer is shedding clouds of spores. Specimen obtained at Munich, Germany. Reduced to ½ natural size.

few weeks but for six whole months! No other fungus, so far as is yet known, sheds spores for anything like so long a time. White made continuous observations on spore-discharge from one and the same fruit-body for the full twelve months of each of the years 1915 and 1916. Spore-traps were set under the fruit-body from early spring until late autumn daily, and during the winter weekly. In addition to this unbroken series of observations during two years on one fruit-body, other observations upon spore-discharge were made upon other fruit-bodies during shorter periods each summer.[1]

White's observations show that, in the neighbourhood of Toronto, Canada, the spore-fall period of *Fomes applanatus* begins

[1] J. H. White, *loc. cit.*, p. 140.



early in May and continues without interruption until the first heavy frost in late October or early November, when it suddenly ends. During this period of approximately six months, the liberation of the spores never ceases and is remarkably uniform (*cf.* Fig. 48). For the first few days after the commencement of spore-fall, the spore-deposit on the slides is rather scanty, but even then can be seen with the naked eye. Soon, however, the daily spore-deposit becomes almost constant; and it remains so for the rest of the spore-fall season. Any increase that may be observed is in the months of July and August.[1]

The daily slide collections for two seasons showed invariably their brown coating of spores. Changing slides at regular intervals throughout the day, and even throughout the night, gave no indication of any periodicity of discharge: the liberation of the spores continued steadily throughout the spore-fall period. On a still day White saw, just as I did for *Polyporus squamosus*,[2] the spores

FIG. 49.—*Fomes applanatus*. Diagram to show the mode of escape of the spores from the hymenial tubes. A, vertical section through four tubes of a fruit-body attached to a tree. The tubes have grown directly toward the centre of the earth so that the long axis of each is perpendicular. In each tube the spores are shot from the hymenium into the centre of the cavity and then fall down vertically in still air until they emerge from the pore. The trajectories of a few spores are shown by the arrows. B, a similar tube represented as tilted through an angle of 1°. As shown by the arrows at *a* and *b*, all the spores discharged above *c*, *i.e.* in the upper five-sixths of the tube, hit and stick to the tube's side, and are lost. Only at and below *c* can the spores escape freely. C, a cross-section through a hymenial tube-layer.

[1] J. H. White, *loc. cit.*, p. 140.

[2] *Researches on Fungi*, vol. i, 1909, p. 90.

drifting away from a fruit-body in curling clouds like wreaths of very fine smoke as long as he cared to watch them ; and such clouds were observed as late as October 15. Night examinations of the spore-clouds were made with a lantern.[1] The discharge of the spores did not appear to be affected by variations in light, humidity of the air, or change in temperature within very wide limits. However, frost caused an instant cessation of spore-discharge and, thereafter, no further fall of spores took place until a new set of hymenial tubes was organised in the spring.[2]

At the Spring Foray of the British Mycological Society held at Haslemere, May 14, 1921, on ascending a steep slope, a fallen log was observed from which projected a large fruit-body of *Fomes applanatus*. Upon looking at the fruit-body, the members saw spores emerging from its under side and floating away in the sunlight.[3] At Kew Gardens, in the autumn of the same year. I found a large fruit-body of *Fomes applanatus*, about 1 foot from the ground, roofing over the space between two large buttress-roots of a Beech tree. On watching the exit of the hole under the fruit-body, with the aid of diffuse daylight only, I distinctly saw brown spore-clouds drifting outwards at intervals ; and I repeated this observation on August 29, September 9, and on several days in between those dates. It was then necessary for me to leave Kew. After my departure and at my request, Mr. S. Dickinson visited the tree on October 16 and a week later on October 23 ; and he kindly reported to me that on both occasions he clearly saw spore-clouds emerging from beneath the pileus. Thereafter in 1921 no further observations were made. In the following year, 1922, I observed spore-clouds coming away from the same fungus on June 17, August 1, and September 4. The evidence thus obtained goes to show that in England the spore-fall period of *Fomes applanatus* extends from early in May until late in October, *i.e.* for nearly six months. It is possible that, in England, owing to the milder climate, the spore-discharge period of this species may be even more prolonged than in Canada.

Observations upon the Kew fruit-body just described convinced

[1] J. H. White, *loc. cit.*, p. 140.
[2] *Ibid.*, pp. 141, 167.
[3] *Trans. Brit. Myc. Soc.*, vol. vii, 1922, p. 221.

me that the numbers of spores coming away from the fruit-body each day was enormous. Near the fruit-body the bark of the tree and the leaves on the ground beneath had become coated with a brown layer of spores; but direct inspection of the escaping spore-clouds indicated that this spore-deposit only represented a very small fraction of the total number of spores actually produced. On the other side of the Beech a fruit-body was found roofing over a long narrow radial hole in the tree-trunk (*cf.* Fig. 50). From this hole the spores could not so easily escape owing to its form and the smallness of the opening. Hence they had accumulated beneath the pileus. The brown spore-deposit there present was so thick that I had no difficulty in filling a wooden match-box with it. When full, the match-box doubtless contained many thousands of millions of spores.

FIG. 50.—*Fomes applanatus*. A fruit-body with about nine annual hymenial tube-layers, and therefore about nine years old, roofing over a hole in the base of a tree. On the floor of such a hole the spores often accumulate as a thick brown layer. Photographed in Mulgrave Woods, Yorkshire, by A. E. Peck. About ½ natural size.

A Comparison of the Spore-fall Period of Certain Hymenomycetes.- The length of the spore-fall period for a number of Hymenomycetes, together with indications as to the mechanical

consistence of each kind of fruit-body, etc., is given in the following Table.

Length of the Spore-fall Period in Hymenomycetes.

	Species.	Spore-fall Period.	Mechanical Consistence.	Attached to or Severed from Substratum.	Observer.
Agaricineae	Coprinus curtus				
	Small fruit-body	35 minutes	Very watery	Attached	Buller
	Large fruit-body	2 hrs. 25 min.	Very watery	,,	,,
	Coprinus sterquilinus	8–12 hours	Watery	,,	,,
	Coprinus comatus	2 days	Less watery	,,	,,
	Psalliota campestris	7 days	Firm	,,	,,
	Stropharia semiglobata	7 days	Firm	,,	,,
	Panaeolus campanulatus	10 days	Firm	,,	,,
	Schizophyllum commune	16 days	Leathery	Severed	,,
	Pleurotus ulmarius	17 days	Tough	,,	,,
Polyporeae	Polystictus versicolor	upwards of 16 days	Leathery	,,	,,
	Polyporus squamosus	14–21 days	Very tough	Attached	,,
	Fomes fomentarius	4–6 weeks [1]	Woody	,,	Faull
	Fomes applanatus	6 months	Woody	,,	White

From the data embodied in the Table one may conclude: (1) that the range of the spore-discharge period for the Hymenomycetes in general is from about an hour, as in *Coprinus curtus*, to about six months, as in *Fomes applanatus*; (2) that the rigidity of a fruit-body and the length of its spore-discharge period are more or less directly correlated, the shortest spore-discharge period being associated with the softest fleshed Agaricineae (the Coprini) and the longest period with the hardest fleshed Polyporeae (species of Fomes), moderately rigid species (Psalliota, Panaeolus, Stropharia) having a spore-discharge period of medium length only; (3) that the genus Fomes is characterised by having a very long spore-discharge period; and (4) that of all the species of Hymenomycetes so far investigated *Fomes applanatus* has by far the longest spore-discharge period.

The Mechanical Consistence of Coprinus and Fomes Fruit-bodies Contrasted.—It is interesting to note how beautifully the mechanical consistence of a fruit-body is adapted to the

[1] Information kindly sent to me in a letter by J. H. Faull.

fruit-body's requirements. The longer the spore-discharge period, the longer must the fruit-body maintain its hymenial layer in the correct position for the discharge of the spores from the basidia, and the greater the risk from drought, the wind, falling leaves and twigs, the visits of animals, etc. It seems therefore only in accordance with the fitness of things that the longer a fruit-body functions, the more mechanically resistant shall be its structure. The watery consistence of a Coprinus is all that is needed for a fruit-body which, in the expanded condition, is to function for a few hours only or at most for a couple of days. A Coprinus fruit-body with the consistence of a Fomes would be a mechanical absurdity, embodying a waste both of material and of energy. On the other hand, an exceedingly hard and woody frame is just what is required for the perennial fruit-body of a Fomes, which is destined to shed showers of spores from long and narrow hymenial tubes for 5, 10, 20, 40 and, in some instances, for 80 years in succession. During the passage of the years the fruit-bodies of *Fomes applanatus*, *F. igniarius*, *F. fomentarius*, *F. officinalis*, etc., must withstand the most violent gales of wind, the fall of branches, twigs, and leaves, the pressure of the winter's snow, the pelting of hail-stones, and the visits of birds, squirrels, etc. If they had the watery consistence of a Coprinus, they would be mechanical failures ; for they would not be able to hold their fine tubes in exactly vertical positions for any great length of time, and they would be ruined by external agencies within a few weeks of their appearance.

In my student days, whilst wandering in an ancient wood near Leipzig, I observed two large fruit-bodies of *Fomes igniarius* projecting from the bole of an Oak tree, and I was much struck with the discovery that they were so hard and so firmly attached that I was unable to detach them and take them home as specimens. I wondered why they were so rigid and so tightly fixed to their substratum, and whether or not Nature had not been a little over-generous in bestowing upon them the gift of rigidity in so extraordinary a degree ; but Nature has now whispered her secret into my ear. It is evident that the rigidity and fixity of all the Fomes species are strictly correlated with the mechanical

requirements of the fruit-bodies during their many years of spore-producing activity.

The Number of Spores in Fomes applanatus and Other Basidiomycetes. —The total number of spores liberated by a large fruit-body of *Fomes applanatus* during the six months of its spore-fall period is enormous—far greater than that of *Polyporus squamosus* or of any of the fleshy Agaricineae so far investigated and of the same order as that of a large Giant Puff-ball (*Calvatia gigantea*). This conclusion is based on the following facts and considerations.

(1) J. H. White, using my haemocytometer method, observed that a *Fomes applanatus* fruit-body having a pored area equal to about one square foot liberated 30,000,000,000 spores in 24 hours; and he also observed that the length of the spore-fall period was six months and that, during this period, the number of spores liberated per day, as judged by the diurnal spore-deposit, was very constant.[1] Granting, then, that 30,000,000,000 spores were liberated each day for six months, the total number of spores which the fruit-body liberated must have been approximately 182 × 30,000,000,000 or 5,460,000,000,000.

(2) The total number of spores produced by a large fruit-body of *Coprinus comatus* was calculated as follows. The number of spores on 0·01 of a square millimetre of gill-surface was counted, and the total area of the hymenial surface on all the gills was measured. A simple calculation based on these data then showed that the fruit-body had developed on its gills approximately 5,240,000,000 spores.[2] These spores, had they been left undisturbed, would have been liberated in about 48 hours. It is clear, therefore, that the total number of spores produced by a large fruit-body of *Coprinus comatus* during the two days of its spore-discharging activity is only about one-thousandth of the total number of spores produced by a large *Fomes applanatus* fruit-body in six months.

(3) By using a method essentially similar to that just described for the investigation upon *Coprinus comatus*, I found that a Mushroom (*Psalliota campestris*) about 4 inches in diameter produced

[1] J. H. White, *loc. cit.*, pp. 139–142.

[2] A. H. R. Buller, *Researches on Fungi*, vol. i, 1909, pp. 82–83.

about 16,000,000,000,000 spores.[1] These, if the Mushroom had been left undisturbed, would have been liberated in about six days. It thus appears that a large Mushroom liberates in about six days only about one three-hundred-and-thirtieth of the number of spores produced by a large *Fomes applanatus* fruit-body in six months.

(4) A fruit-body of *Polyporus squamosus*, as estimated by the haemocytometer method, produced 44,450,000 spores from one square centimetre of its pored surface in about a week, the fungus having been separated from the tree on which it grew. Taking the area of the fruit-body as 250 square centimetres (many fruit-bodies of this species have a much larger area than this), the total number of spores which the fruit-body produced must have been about 11,000,000,000.[2] A fruit-body of *Polyporus squamosus*, as large as the fruit-body of *Fomes applanatus* investigated by White, with the same basis of calculation as before, would have shed 44,450,000,000. I suspect, however, that this total is somewhat too small, for the spores of the spore-deposit were collected under artificial conditions and during a period which must have been several days shorter than the full spore-discharge period.[3] It would, I think, be safe to say that a large fruit-body of *Polyporus squamosus* produces at least 50,000,000,000 in the fourteen to twenty-one days of its spore-discharge period. This great total, however, is only about one-hundredth of the total number of spores produced by White's large *Fomes applanatus* fruit-body in six months.

(5) A fruit-body of *Daedalea confragosa*, severed from a log of wood and having a pored area of about 2 square inches only, shed during its spore-discharge period of one week 682,000,000 spores,[4]

[1] *Vide infra*, Chap. XIII, Section: "The Spore-discharge Period and the Number of Spores."

[2] A. H. R. Buller, *Researches on Fungi*, vol. i, 1909, p. 83.

[3] The full spore-fall period for a large fruit-body of *Polyporus squamosus* under favourable conditions is from about 14 to 21 days. *Vide* these *Researches*, vol. i, 1909, pp. 90–92. F. T. Brooks ("Notes on *Polyporus squamosus*," *The New Phytologist*, vol. viii, 1909, p. 350) at Cambridge, England, saw spore-clouds issuing from a large fruit-body for ten days after full growth of the pileus had been completed. Doubtless, however, spores were liberated for a few days before the spore-clouds became visible.

[4] These *Researches*, vol. i, 1909, p. 85.

i.e. one eight-thousandth of the total number of spores shed by White's large *Fomes applanatus* fruit-body in six months.

(6) A large fruit-body of *Coprinus sterquilinus*, which was investigated in the same manner as the fruit-body of *C. comatus* already described, was found to have produced a total of about 100,000,000 spores only.[1] These, if left undisturbed, would have been liberated in about eight hours. The total number of spores liberated by a large *Coprinus sterquilinus* fruit-body in about eight hours is only about one fifty-four-thousandth of the total number of spores liberated by White's large *Fomes applanatus* fruit-body in six months.

(7) Finally, a large Giant Puff-ball (*Calvatia gigantea*) was found to contain about 7,000,000,000,000 spores,[2] *i.e.* about 1,500,000,000,000 more spores than were liberated in six months by White's large *Fomes applanatus* fruit-body.

The data given above for the total number of spores produced and the length of the spore-fall period for each species, together with the results of calculations for the number of spores liberated per day, are embodied in the following Table. The actual figures can only be considered as approximately correct.

Spore-discharge Data for the Giant Puff-ball and Certain Hymenomycetes.

Species.	Total Number of Spores.	Size of Fruit-body.	Spore-fall Period.	Number of Spores Discharged per Day.
Calvatia gigantea .	7,000,000,000,000	large	...	...
Fomes applanatus .	5,460,000,000,000	large	6 months	30,000,000,000
Polyporus squamosus .	50,000,000,000	large	14 days	3,571,000,000
Psalliota campestris .	16,000,000,000	large	6 days	2,666,000,000
Coprinus comatus .	5,240,000,000	large	2 days	2,620,000,000
Daedalea confragosa .	682,000,000	2 sq. in.	7 days	97,000,000
Coprinus sterquilinus .	100,000,000	large	8 hours	100,000,000

We may now ask: why is it that a large *Fomes applanatus* fruit-body produces several hundred times as many spores as a large Mushroom (*Psalliota campestris*)? I believe that the answer to the question is to be found chiefly in the fact that the area of the hymenium of the Fomes fruit-body is far greater than the

[1] *Vide infra*, vol. iii, Chap. VIII, *Coprinus sterquilinus*, Section: "The Spores."

[2] These *Researches*, vol. i, 1909, pp. 85–86.

corresponding area of the Mushroom. I found that a wild Mushroom about 4 inches in diameter has a hymenial area of about 1·33 feet and produces about 16,000,000,000 spores.[1] Now White's large *Fomes applanatus* fruit-body had a pored area of about 1 square foot. It is therefore clear that the hymenial area of the Mushroom is only slightly larger than the area of the under side of the Fomes. I showed in Volume I that in *Fomes applanatus* (= *F. vegetus*), owing to the disposition of the hymenium in the inside of very fine closely-packed tubes, with a tube length of 12 mm. the specific increase of hymenial surface is 148, *i.e.* that a *Fomes applanatus* fruit-body with a tube depth of 12 mm. and a pored area of 1 square foot has a hymenial area of about 148 feet.[2] Now in some large fruit-bodies, *e.g.* the one shown in Fig. 48, p. 131, the tubes may be 18 mm. deep or even deeper. Let us assume that White's large fruit-body had a tube depth of 18 mm. Then the specific increase of hymenium would be 220, *i.e.* the hymenial area would be 220 square feet. We therefore see that :

$$\frac{\text{The hymenial area of the Fomes}}{\text{The hymenial area of the Mushroom}} = \frac{220}{1\cdot33} = 165,$$

i.e. that White's *Fomes applanatus* fruit-body had a hymenial area about 165 times greater than that of our Mushroom.

Now let us imagine a Mushroom so big that it has a hymenial area not of 1·33 feet but of 220 feet, *i.e.* a hymenial area equal to that of White's *Fomes applanatus*. How many spores would it produce ? Since a Mushroom with a hymenial area of 1·33 produces, as we have seen, 16,000,000,000 spores, a Mushroom with 220 feet of hymenial area would produce :

$$\frac{220}{1\cdot33} \times \frac{16{,}000{,}000{,}000}{1} = 2{,}640{,}000{,}000{,}000 \text{ spores.}$$

Now the *Fomes applanatus* fruit-body with a hymenial area of 220 square feet produced, as we have seen, about 5,460,000,000,000. This number is only about twice that obtained for the Mushroom, *i.e.* is of *the same order as that number*.

[1] *Vide infra*, Chap. XIII, Section : "The Spore-discharge Period and the Number of Spores."

[2] Vol. i, 1909, p. 32.

The foregoing calculations are in conformity with the view that there is no fundamental difference in the structure of the hymenium of a Mushroom and of *Fomes applanatus*, and that the chief reason why a *Fomes applanatus* fruit-body produces some three hundred and thirty times as many spores as a large Mushroom is that the hymenial area of the former is about 165 times greater than that of the latter. I have observed that, in *Panaeolus campanulatus*, *Stropharia semiglobata*, *Psalliota campestris*, and in the Hymenomycetes generally, the hymenium contains, from its first origin and before a single spore is developed, a definite limited number of rudimentary basidia destined to produce and liberate spores during the course of the spore-discharge period.[1] The basidia ripen and shed their spores in succession, and spore-discharge ceases as soon as the pre-formed basidial elements have become exhausted. Each square millimetre of any hymenium can develop a certain number of spores only and no more. The exact number varies with each species and is affected by the size and packing of the basidia, species having large basidia and correspondingly large spores producing per unit of hymenial area fewer spores than species having small basidia with correspondingly small spores.

The Cause of the Long Spore-discharge Period in Fomes applanatus.—Granted that the structure of the hymenium of *Fomes applanatus* does not differ essentially from that of the Agaricineae, how comes it, one may ask, that, whereas the Agaricineae shed all their spores in about six to eighteen days, a *Fomes applanatus* fruit-body goes on shedding spores for about six months? It seems to me that the answer to this question is to be sought in the difference in the mode of development of the structures which support the hymenium, *i.e.* of the gills in the Agaricineae and of the hymenial tubes in *Fomes applanatus*. In what follows let us think of the Common Mushroom, *Psalliota campestris*, as representing the Agaricineae.

After a Mushroom has developed its gills up to the stage when the pileus is just beginning to expand, no new basidial elements are added to the hymenial layers. As the pileus expands, it is true that the two hymenial layers covering the two sides of each

[1] *Vide infra.*

gill do increase somewhat in area ; but this increase is due merely to the increase in size of the individual basidia and paraphyses and not to their multiplication. After the expansion of the pileus, the hymenial layers on each gill remain quite constant in area until the end of the spore-discharge period, *i.e.* until they have used up their basidia in spore-formation and spore-discharge. The gills of a Mushroom, after the expansion of the pileus, do not grow in depth and therefore do not add to themselves progressively new hymenial areas. The result is that all the square millimetres of the hymenial layers of a Mushroom begin and end their spore-discharge period at about the same time.

In *Fomes applanatus*, on the other hand, the hymenial tubes are not developed throughout their whole length from the first, but *elongate slowly for many weeks or even months*. The cavities of the tubes, when first formed, are merely hemispherical in shape. The coalescent rims of these cavities then simultaneously all grow vertically downwards, so that the cavities soon become shaped like those of inverted cups and, finally, like those of inverted test-tubes. White observed that, by the time the tubes had become about 1·5 mm. ("1/16 inch") long in the first or second week of May, the fall of spores had begun.[1] This indicates that the hymenium lining the inner surfaces of the tubes is developed, just as in *Polyporus squamosus*,[2] *pari passu* with the growth in length of the tubes. By the end of July, White found that the tubes had become 9·4 mm. long ("3/8 inch") and that after this time their growth in length "slowed down considerably, gradually becoming imperceptible."[3] We thus have direct evidence that the tubes grow in length for the major part of the six-month spore-discharge period. As the tubes grow in length at their pored ends only, they progressively add new areas to the hymenium ; and, doubtless, each new area so added takes several weeks to exhaust its basidia and shed all its spores. It seems to me, therefore, that the

[1] J. H. White, *loc. cit.*, p. 139. [2] Vol. i, 1909, p. 92.

[3] J. H. White, *loc. cit.*, p. 139. White, unfortunately, does not record the final length of the tubes in October. It is to be hoped that someone will determine the rate of growth per week of the hymenial tubes of *Fomes applanatus*, *F. igniarius*, *F. fomentarius*, etc., and present to us the results of his work in the form of graphs.

great length of the spore-discharge period of *Fomes applanatus* is due, in part at least, to the fact that the hymenial tubes grow continuously in length for several months and thus continuously develop entirely new stretches of hymenium on their interior. There is nothing in the growth of the gills of Agaricineae to correspond to the slow elongation of the tubes of *Fomes applanatus*. Hence it is that the spore-discharge period of the Common Mushroom, of *Pleurotus ulmarius*, etc., has a length of only about six to eighteen days, whereas that of *Fomes applanatus* has a length of six months.

The Progressive Exhaustion of the Hymenial Tubes.—It is not unlikely that, toward the end of the annual spore-fall period of *Fomes applanatus*, the lower part of the hymenium in each tube, *i.e.* the part most recently developed, is liberating spores most rapidly, whilst the upper older part is liberating spores either very slowly or not at all owing to the exhaustion of most of its basidia. If this surmise is correct, it would accord with the fact that, notwithstanding the progressive increase in the total area of the hymenium of a fruit-body, the diurnal spore-deposits, as observed by White, were remarkably uniform throughout the spore-fall period. It would also accord with what we know concerning the gradual exhaustion of the hymenia of *Panaeolus campanulatus*, *Stropharia semiglobata*, *Psalliota campestris*, etc.[1] I suspect, therefore, that the hymenium of each tube of *Fomes applanatus* exhausts itself progressively from above downwards and that the rate of its exhaustion is correlated, to some extent at least, with the rate of the elongation of the tube in which it has developed.

I have attempted to obtain evidence of the progressive exhaustion of the hymenial tubes from above downwards, but so far without success. On September 3, 1921, from the Kew fruit-body already described, a piece of the most recently organised annual tube-layer was obtained and found in one place to be 25 mm. (1 inch) deep. From a block of hymenial tubes having this depth, transverse sections were cut at intervals from below upwards and examined with the low power of the microscope. It was ascertained that spores were still being produced and liberated in certain

[1] *Vide infra*, Chapters X, XI, XII, and XIII.

of the tubes all the way down, from the top to the bottom, except the last 3 mm., where, apparently, growth in length was still proceeding. No actual sign of exhaustion of the hymenium in each tube from above downwards was therefore observed; but the tubes may not have been studied late enough in the year. On the other hand, it is possible that the hymenium of *Fomes applanatus* is organised in a different manner from that of the Agaricineae and that interesting discoveries in this connection may await the careful investigator.[1]

The Significance of the Production of Vast Numbers of Spores.—As we have seen, many of the larger Hymenomycetes, *e.g. Fomes applanatus*, *Polyporus squamosus*, *Psalliota campestris*, etc., liberate many thousands of millions of spores during their spore-fall period. Since the number of plants of any hymenomycetous species remains fairly constant from year to year, it is clear that for every spore of *Fomes applanatus*, *Polyporus squamosus*, *Psalliota campestris*, etc., which succeeds in germinating and in establishing a flourishing sporophore-producing mycelium, some thousands of millions of spores must fail. This fact suggests an enquiry into the significance of spore numbers. What advantage accrues to Hymenomycetes from the production and liberation of vast quantities of spores most of which are doomed to die either before or after germination without producing a fruiting mycelium? Is not the production and liberation of spores by thousands of millions a wasteful process? We shall now attempt to answer these questions.

Let us, in order to be concrete, consider the production of spores by *Fomes applanatus*. This fungus, as we have seen, is a wound-

[1] In certain large, rapidly developing species of Polyporus, *e.g. Polyporus squamosus* (*vide* the longitudinal spore-deposit shown in vol. i, Plate IV, Fig. 28), *P. hispidus* (tubes up to about 20 mm. long), *P. cuticularis* (tubes 8 mm. long), the hymenial tubes, when about full-grown, produce and liberate spores throughout their whole length, except close to their apertures. Whether, toward the very end of the spore-fall period, they show any signs of exhaustion from above downwards, I have not as yet ascertained. If they do not, since hymenial tubes begin to shed spores soon after they begin to grow downwards and elongate basally for a week or more, it seems likely that the number of spores ultimately produced and liberated by each unit of area of the hymenium in any tube must be greatest at the top of the tube, must be least at the bottom, and must decrease in the tube from above downwards. Further investigations alone can teach us the truth about this matter.

parasite and lives on the wood of the trunks, thick branches, and stumps of forest trees ; and it also produces many thousands of millions of spores each day for about six months of each year. Let us imagine that this fungus has established itself in a tree-trunk in a virgin forest, such as we find in western Ontario, and let us suppose that it has developed a large fruit-body on the tree's exterior. The fruit-body will pour out daily from its hymenial tubes some thousands of millions of spores. What new trees can be infected by these spores ? Certainly not each and every one. The bark of a tree, composed, as it largely is, of sheets of cork, and containing, as it does, various special chemical bodies such as tannin, resin, etc., protects the tree's inner tissues from the invasions of parasitic fungi and, in particular, so far as our present enquiry is concerned, from the attacks of wood-destroying fungi. We are therefore safe in assuming that our Fomes cannot gain a new foothold on any tree which has uninjured bark.

From the foregoing we are forced to the conclusion that the invasions of our Fomes must be limited to trees with wounds, *i.e.* trees which have had their bark injured and their wood exposed in open wounds through the breaking of branches by the wind, through frost-cracks, strokes of lightning, the fall of dead branches projecting from the tree-trunk, the fall of neighbouring trees, etc. Now in all probability, it is only the larger wounds of a tree that can be used as entrance places by our Fomes. I suspect that no large wood-destroying fungus can enter a tree through very small wounds, such as are made when dead twigs fall from the higher branches and when thin but still living branches are broken from a tree by accident. In most trees, as one may readily realise by observing their growth in successive years, most of the twigs are doomed to die before they become many years old ; and, if one examines the forest floor under Oaks, Beeches, Elms, etc., one finds that it becomes littered every year not merely with the dead leaves but with a great number of dead twigs which have died a perfectly natural death and have been shed by the higher branches. Now if a wound-parasite, like our *Fomes applanatus*, could obtain entry into the thicker branches and the trunks of trees through small wounds made by the fall of dead twigs and the breaking away of

small thin living branches, it is probable that all the trees in a forest would become infected with wood-destroying fungi very early in life. But this we know is not usually so and we often find trees in old forests which have lived for scores or even hundreds of years, which have shed tens of thousands of small twigs, and which yet have perfectly sound trunks and main branches. Let us assume therefore that our Fomes only enters a tree *via* large wounds made by the removal of bark from the trunk and thick limbs and by the breaking away of stout branches.

What chance have the spores of a fruit-body of *Fomes applanatus* to settle upon tree-wounds that can be infected ? In a square mile of forest the number of trees with infectible wounds must be strictly limited ; and the total area of these wounds must indeed be very small relatively to the square mile of forest. Let us assume that this total area of infectible wound-surface is 100 square feet. Then the barren area relatively to the infectible area in the square mile of forest would be roughly :

$$\frac{28{,}000{,}000}{100} = 280{,}000.$$

Supposing therefore that the spores of the fruit-body of *Fomes applanatus* were dispersed by the wind so that they settled fairly evenly over the square mile of forest, the chances that any given spore liberated by the fruit-body would settle on an infectible wound-surface would be 280,000 to 1 against. But our assumptions have been too favourable to the chances of spore-dissemination, for the wounds would often be more or less vertical or even looking downwards rather than strictly horizontal and looking upwards, and it is probable that, owing to periodic rainfall and stillness of the atmosphere and to leaf-screens, etc., the odds are considerably against any particular spore being carried even half a mile from its parent fruit-body before reaching the earth. The mathematical calculation given above is based on assumptions which can be only more or less true, but I think that it is sufficiently accurate to indicate that the chances of any particular spore settling upon an infectible wound-surface in a forest are millions to one against. This being granted, it is clear that, if the spores of our *Fomes*

applanatus fruit-body are to reach infectible wounds in a forest, they must be produced by the million.

When a tree has received a serious wound, the way is usually open for the attack on the wood, not by one wood-destroying fungus only but by several. Which species, other things being equal, is the one most likely to infect a new wound first ? Surely the one that has the most numerous spores floating about in the air, for the spores of such a fungus are likely to settle on the wound first. The success of one species of wood-destroying fungus rather than another in infecting a particular wound and thus occupying the new substratum to the exclusion of competitors, may often be simply a question of a few hours or days of priority in spore-arrival.

Which individual *Fomes applanatus* plants are most likely to give rise to successful progeny ? Other things being equal, surely those which develop fruit-bodies most freely and the fruit-bodies of which have the maximum efficiency in producing spores ; for, the more spores a plant produces, the greater will be its chance of beating its competitors of the same species in the struggle for existence.

In order to occupy a new wound-surface successfully, it is advantageous for any fungus plant to deposit on that surface as many spores as possible, for thereby the wound will become infected in many places, and, from the first, a vigorous mycelium will be present. This is all to the good in the struggle for existence of the plant with other fungus plants either of the same species or of other species. It may therefore be said that, other things being equal, the more spores a given fungus plant can cause to settle on a given infectible wound-surface, the greater will be the chance of survival for its progeny. We thus again perceive an advantage in such a fungus as *Fomes applanatus* producing vast numbers of spores.

From the experiments made by Kniep [1] and others [2] with about thirty diverse species, it seems probable that the majority of Hymenomycetes, like the majority of Mucorineae, are heterothallic. It is also known that in heterothallic species of Hymenomycetes

[1] Hans Kniep, "Über morphologische und physiologische Geschlechts-differenzierung," *Verhandl. der Physikal.-med. Gesellschaft zu Würzburg*, 1919, pp. 12, 13.

[2] Irene Mounce, "Homothallism and Heterothallism in the Genus Coprinus," *Trans. Brit. Myc. Soc.*, vol. vii, 1922, pp. 256–269.

the formation of fruit-bodies takes place much more readily and perfectly from secondary mycelia produced by the union of two mycelia of opposite sex than from individual primary mycelia, each of which has originated from a single spore and is unisexual.[1] Some wood-destroying fungi, *e.g. Schizophyllum commune*, *Stereum purpureum* and *Armillaria mucida*, are known to be heterothallic,[2] and it may well be that heterothallism prevails in the genus Fomes. It is therefore not unlikely that *Fomes applanatus* is heterothallic. If it is, the production by its fruit-bodies of vast numbers of spores would not only increase the chance of multiple infection of a wound-surface on a tree, but also make it possible for spores of opposite sex to germinate near to one another and thus produce secondary mycelia of full fruiting capacity.

From the foregoing discussion we may conclude that the daily production of thousands of millions of spores by the fruit-bodies of *Fomes applanatus* and of other wood-destroying fungi is not essentially a waste of reproductive energy, but is necessary and distinctly advantageous to the species concerned, owing : (1) to the fact that the probability of any particular spore being carried by the wind to substrata suitable for germination rather than to substrata unsuitable for germination is excessively small ; (2) to the fact that, in the struggle for the occupation of new substrata suitable for growth and reproduction, each plant must compete with other fungus plants of the same species and of other species, and (3) to the likelihood that the fungi are heterothallic and that only secondary mycelia produced by the union of two primary mycelia of opposite sex can produce fruit-bodies in a normal manner.

Finally, for the Hymenomycetes in general, it seems probable that the number of spores produced by the fungus plants is correlated roughly : (1) with the nature of the difficulties encountered by the spores in passing from their parent fruit-bodies to suitable substrata, (2) with the amount of competition from other organisms which must be met with in the struggle for existence, and (3) with the requirements of sex.

[1] Irene Mounce, *loc. cit.*

[2] H. Kniep, *loc. cit.*

CHAPTER VI

SPORE-DISCHARGE IN THE HYDNEAE, TREMELLINEAE, CLAVARIEAE, AND EXOBASIDIEAE

Preliminary Remarks—Spore-discharge in the Hydneae—Spore-discharge in the Tremellineae—The Basidial and Oidial Fruit-bodies of *Dacryomyces deliquescens*—Spore-discharge in the Clavarieae—The Genus Calocera—Spore-discharge in the Exobasidieae

Preliminary Remarks.—The following are the main groups of the Hymenomycetes :

Tremellineae	Hydneae
Clavarieae	Polyporeae
Thelephoreae	Agaricineae
Exobasidieae	

The investigations upon the production and liberation of the spores of Hymenomycetes so far recorded in the pages of this work were made upon the Agaricineae, the Polyporeae, and the Thelephoreae. The object of this Chapter is to treat of the production and liberation of spores in the remaining groups of Hymenomycetes, namely, the Hydneae, the Tremellineae, the Clavarieae, and the Exobasidieae.

The relation of structure to function in the fruit-bodies of the Agaricineae, although the subject of many remarks in Volume I, is dealt with in this second Volume in various places, particularly in the descriptions of the Sub-types of organisation in the Agaricineae ; and some special observations on the mechanical significance of the stipe, the pileus-flesh, and the gills of *Psalliota campestris*, which are of wide application, will be found in the Chapter devoted to that species. For some further observations in this Volume upon spore-discharge in the Polyporeae and

Thelephoreae the reader should consult the references given in the Index.

In what follows, on account of the fact that several well-known Hydneae, *e.g. Hydnum repandum*, greatly resemble terrestrial Agaricineae in their general form, I shall treat of the Hydneae before the Tremellineae.

Spore-discharge in the Hydneae. —The Hydneae are characterised

Fig. 51.—*Hydnum repandum*, a terrestrial Hydnum with a centric stipe. Its hymenial spines are positively geotropic and point vertically downwards. Photographed in leaf-mould at Epping Forest, Essex, by Somerville Hastings. About $\frac{2}{3}$ natural size.

by having the under sides of their pilei produced into sharply pointed spinous processes (Figs. 51, 53–55). These processes, just like the gills in the Agaricineae and the tubes in the Polyporeae, serve to increase the surface area of the under side of the pileus and therefore also the area of the hymenium which covers it. Thus the spines, just like gills and tubes, serve to increase the number of spores which a pileus of any given size is able to develop.

The spines of *Hydnum repandum* (Fig. 51) and of other Hydna with centric stipes, like the tubes of the Boleti, begin their development before the pileus expands and grow out perpendicularly from the under surface of the pileus-flesh. The expansion of the

pileus brings the long axes of all the partially developed spines into positions which are more or less perpendicular to the surface of the earth. After the expansion of the pileus, the spines continue their growth in length and become positively geotropic. By responding to the stimulus given by the earth's mass, they bring their axes into exactly vertical positions with respect to the earth's surface. In Hydna with centric stipes, the spines, just like the tubes of the Boleti, are brought into their right positions in space by two adjustments—a coarse one consisting of the expansion of the pileus, and a fine one consisting of the reaction of each spine to the stimulus of gravity. The fine adjustment causes the hymenium on the sides of the spines to look slightly downwards toward the earth in the same manner as the hymenium on the sides of gills; and a median vertical section through a straight spine of *Hydnum imbricatum*, *H. septentrionale* (Figs. 53, 54), *H. erinaceus* (Fig. 55), *H. coralloides*, etc., resembles in its wedge-shaped form a transverse vertical section through a gill of *Psalliota campestris* or an Amanita. Spines, gills, and hymenial tubes on the under side of a pileus are all highly efficient means of increasing hymenial surface without loss of compactness for the fruit-body as a whole; and in general they are so constructed that their free surfaces, and therefore also their hymenial coverings, look either slightly downwards toward the earth or horizontally. Thus provision is made for interspinal, interlamellar, and intratubular spaces of such a form as to favour the escape of the spores when these have been shot outwards from the hymenium and are falling vertically.

The basidia of the Hydneae discharge their spores in the same manner as other Hymenomycetes. Just before the discharge of a spore, a drop of water is excreted at the hilum and, when discharge takes place, the spore is violently shot forward into an interspinal space to a distance of about 0·1 mm. After travelling this distance, the spore makes a sharp turn from a horizontal to a vertical direction and then falls slowly downwards with a steady terminal velocity between the spines. The sporabolas of a Hydnum and of a Psalliota are identical in form.

The excretion of a drop of fluid at the hilum of a spore a few

FIG. 52. —*Hydnum septentrionale* Fr. Fruit-bodies springing from a frost-crack in the trunk of a Manitoban Maple, *Acer Negundo*. This species is said by Fries to be the largest of all Hydna. Its pilei are dimidiate, caespitose, and creamy-white. The central mass was 5 inches broad and 8 inches high. Photographed by C. W. Lowe in Elm Park, Winnipeg. Somewhat less than $\frac{1}{2}$ natural size.

seconds before discharge was observed in *Hydnum imbricatum* and in a leathery species common in the woods at Minaki

FIG. 53.—*Hydnum septentrionale* Fr. The upper fruit-body mass of Fig. 52. The hymenial teeth are positively geotropic and point toward the earth's centre. Natural size.

(on the Winnipeg River), which appeared to be either *H. ferrugineum* or a close relative. To observe the drops, sections of

a pileus including some uninjured spines were placed in a closed moist compressor cell, and various basidia were watched with the microscope. Owing to the crowding of the basidia, the small size and slow development of the spores, and other difficulties, a long-continued study of the sections was required before any successful observations could be made. The investigation of *Hydnum imbricatum* cost six hours and that of *H. ferrugineum* four hours, whereas similar investigations upon Agaricineae can usually be brought to a successful conclusion in less than an hour.

Fig. 54.—*Hydnum septentrionale* Fr. Transverse section through two imbricated pilei of the fruit-body mass shown in Fig. 53. The hymenial teeth are positively geotropic and look vertically downwards. The space between the two pilei permits of the wind sweeping away the spores falling from the teeth of the upper pileus before they can settle on the top of the lower pileus. The longest teeth are 1·1 cm. in length. Natural size.

The illustrations of Hydna here provided show fruit-bodies of: (1) *Hydnum repandum* which commonly occurs in leaf-mould in woods in Europe and North America and has a central stipe and rounded pileus like a Mushroom; (2) *Hydnum septentrionale* which occurs upon tree-trunks in Scandinavia, Canada, and the United States, but not in England, and which in general form resembles a dimidiate Polyporus; and (3) *Hydnum erinaceus* which grows attached to logs of wood, etc., in Europe and North America, and has a relatively reduced pileus-flesh and very large and conspicuous spines. Some remarks upon the great size of the fruit-body masses of *H. septentrionale* and upon

the spore-clouds which they emit have already been made in Chapter IV.[1]

The spines of *Hydnum erinaceus* (Fig. 55) attain a length of

FIG. 55.—*Hydnum erinaceus*, the Hedgehog Fungus. A fruit-body attached to wood. The very long spines are pendulous and point toward the earth's centre. On the left, owing to damage by a slug, the spines have become deflected somewhat from the perpendicular. Photographed in Epping Forest, Middlesex, England, by Somerville Hastings. Natural size.

3–6 cm. and hang down rather close together ; but they are never branched and so never resemble the branches of a compound Clavaria. The branching of a Clavaria does not hinder the escape

[1] Pp. 102–105.

of the spores, for it takes place in an upward direction so that the last-formed branches are the highest, while the escape of the spores is lateral or more or less downwards. On the other hand, if the spines of *Hydnum erinaceus* were branched, since the last-formed branches would be the lowest, the interspinal spaces above the ultimate branches would become more or less blocked with a resulting hindrance to the escape of the spores shot into them. That the spines of Hydna are never branched is exactly what should be expected from the point of view of the mechanical requirements for the escape of the spores.

Spore-discharge in the Tremellineae.—Since the publication of the first Volume of this work I have made a few observations upon the production and liberation of spores in certain Tremellineae. These observations will now be described. The species investigated were as follows :

Tremellineae	Auricularieae	Hirneola auricula-judae
		Auricularia mesenterica
	Tremelleae . .	Exidia albida
	Dacryomyceteae	Dacryomyces deliquescens
		Calocera cornea
		Calocera viscosa

The fruit-bodies of the Tremellineae are distinguished from those of all other Hymenomycetes by their peculiar gelatinous consistence. A cross-section through a tremelloid fruit-body reveals the fact that the hyphae of the flesh are not separated by interhyphal air-spaces, but are connected together by a continuous, transparent, gelatinous matrix made up of the much swollen and confluent, outer, hyphal walls. By analogy, we are justified in assuming that the jelly of tremelloid fruit-bodies is not a mere useless bye-product of metabolism but has a biological function of considerable importance. We may therefore ask ourselves : how does the jelly of the Tremellineae assist the fruit-bodies in their work of producing and liberating spores ? I shall now endeavour to answer this question.

In the first place, it is to be noted that the fruit-bodies of the Tremellineae are all *lignicolous*, *i.e.* they grow on dead sticks,

branches, logs, and tree stumps. However, there are many non-tremelloid hymenomycetous fruit-bodies, *e.g.* those of Stereum, Lenzites, Schizophyllum, and Polystictus, which are also lignicolous and which appear to be particularly well adapted to that mode of existence. Thus there are two types of lignicolous fruit-bodies—the *tremelloid* and the *non-tremelloid*.

In dry weather, dead sticks, branches, etc., dry up rather rapidly. As if to meet and overcome this disadvantage, the tremelloid and non-tremelloid lignicolous fruit-bodies are so constructed that, during drought, they dry up without losing their vitality, and that, upon the advent of rain, they rapidly absorb water, revive, and resume their one dominant function of producing and liberating spores. The re-absorption of water by dried fruit-bodies takes place by one of two physical means : (1) *capillarity* and (2) *imbibition*, the first being characteristic of non-tremelloid fruit-bodies, *e.g.* those of Stereum, Lenzites, Schizophyllum, and Polystictus, and the second characteristic of tremelloid fruit-bodies, *e.g.* Hirneola, Auricularia, Exidia, Dacryomyces, and Calocera.

In non-tremelloid lignicolous fruit-bodies which revive in wet weather after drought there are numerous, large, interconnected air-spaces between the hyphae of the pileus-flesh ; and free water, falling on the pileus, is sucked into these spaces by capillarity. Thus a dried fruit-body of *Lenzites betulina* or *Polystictus hirsutus*, when rain comes, rapidly absorbs and stores free water in its capillary system. On the other hand, as already pointed out, tremelloid fruit-bodies—all of which are lignicolous and revive in wet weather after drought—possess no such interhyphal air-spaces as those just described and therefore cannot absorb water by capillarity. However, the flesh of tremelloid fruit-bodies is composed of a continuous gelatinous matrix in which the living hyphae are embedded. This gelatinous matrix takes the place of a capillary system in the absorption of water, the water being absorbed by imbibition instead of capillarity. When free water comes in contact with a dried gelatinous fruit-body, *e.g.* of *Exidia albida* or *Dacryomyces deliquescens*, the fruit-body rapidly imbibes water at its surface and the water so imbibed is drawn by imbibition

throughout the gelatinous mass ; and more and more water is absorbed until equilibrium of water-content has been established throughout the fruit-body and the limit of imbibition has been reached. During the absorption of water the jelly increases enormously in volume, loses its horniness, and becomes more and more watery in consistence. The jelly constitutes not only a water-absorbing system but also a water reservoir. After dry weather sets in, it supplies water to the living cells of the flesh and hymenium, and keeps them turgid so that, for some time after the fruit-body as a whole has begun to contract as a result of transpiration, the production and liberation of spores can be continued.

From the above discussion I think we are justified in believing that the development of jelly in the fruit-bodies of Tremellineae is an adaptation to a lignicolous habit of existence, and that the jelly enables the fruit-bodies which possess it to absorb and store water rapidly when rain comes after drought.

Among Algae, the thalli of the Fucaceae—especially their terminal fruiting branches—have a very similar structure to the fruit-bodies of the Tremellineae ; for, in the main, they consist of branching and anastomosing, hypha-like cells connected together by, and embedded in, a transparent gelatinous matrix formed from the outer, swollen, confluent layers of the cell-walls. The thalli of the Fucaceae grow upon rocks and, as is well known, are exposed to the air at low tide. Whilst so exposed, particularly in warm sunny weather, the thalli transpire and contract considerably ; but, when the tide rises and the sea-water envelops them again, they rapidly absorb water by imbibition and re-expand. Here, just as in the Tremellineae, where vitality must be retained during the persistence of dry conditions, a gelatinous matrix has been developed which functions by absorbing and storing water rapidly as soon as free water again becomes accessible.

The gelatinous matrix of the fruit-bodies of the Tremellineae, when fully expanded, forms by far the larger part of the fruit-body substance, and the living anastomosing hyphae which it envelops, excepting at and near the hymenium, are relatively few and widely separated. Now the jelly in an expanded fruit-body

consists chiefly of water and, doubtless, few organisms except jelly-fish have as little organic matter in them per unit of volume as the more highly tremelloid Tremellineae. We may therefore regard the gelatinous flesh of species of Tremella, Ulocolla, Exidia, etc., so to speak, as a very cheap form of building material by the use of which the fungi to a large extent sacrifice rigidity for ease of construction, but by means of which the object in view, namely,

FIG. 56.—*Tremella frondosa*, a gelatinous fungus growing on wood and having the surface of its lobes covered with the hymenium, so that many of the basidia are upward-looking. Photographed in Epping Forest, Middlesex, England, by Somerville Hastings. Natural size.

the production of a large free surface for the development of the basidia and basidiospores, is successfully attained.

Gelatinous masses are not relished as food by most animals, and coverings of jelly sometimes serve to protect smaller organisms from being devoured. Thus Stahl showed by experiment that a fish (a species of Macropoda) and the fresh-water snail *Lymnaeus stagnalis* will not touch frogs' eggs covered with their gelatinous envelopes, but will devour these same eggs greedily as soon as the envelopes have been artificially removed.[1] Stahl also showed

[1] E. Stahl, *Pflanzen und Schnecken*, Jena, 1888, p. 82.

by experiment that slugs and snails will not feed upon the gelatinous lichen *Collema granulosum*, the highly gelatinous ball-colonies of the blue-green alga *Nostoc commune*, or the gelatinous winter buds of the Utricularіae.[1] It is not unlikely, therefore, although experiment alone can decide the matter, that the jelly of tremelloid fruit-bodies, in addition to being useful by absorbing and storing water and as a building material, may also serve to protect the fruit-bodies from the devastation of slugs.

It has been stated that tremellaceous fruit-bodies, when supplied with water after desiccation, revive and recommence the production and liberation of spores. I myself have observed this revival in the laboratory for *Auricularia mesenterica* after eight months in the dried condition, for *Hirneola auricula-judae* after five weeks, and for *Exidia albida*, *Dacryomyces deliquescens*, and *Calocera cornea* after a few days or weeks. These observations were incidental, and in none of the species named did I seek to determine the extreme length of time during which the dried fruit-bodies can retain their vitality. In the Tremellineae in general, the vitality of the fruit-bodies, like that of Stereum, Lenzites, Schizophyllum, and Polystictus, is probably always retained for at least a few weeks or months and possibly often for upwards of a year, *i.e.* sufficiently long to enable the fruit-bodies to tide over any normal period of drought occurring under natural conditions.

The mode of spore-discharge in the Tremellineae is similar to that in the Agaricineae and other Hymenomycetes. It is true that the gelatinous matrix of the fruit-body extends into the hymenium. However, the basidia are not thereby hindered from carrying out their functions, for the basidium-bodies, although themselves embedded in jelly, produce sterigmata which pierce the outer surface of the jelly and thus come to project freely beyond it. This enables the basidia to develop and discharge their spores in free air in the manner which is normal for all Hymenomycetes.

The fruit-bodies of the Tremellineae, like non-tremelloid fruit-bodies which revive in moist weather after desiccation, possess basidia which develop and ripen their spores very rapidly. Thus

[1] *Loc. cit.*, pp. 80–81.

the average time taken for the development and ripening of an individual spore, from the moment that the spore appears on the sterigma as a tiny rudiment until the moment of discharge, was observed to be: for *Calocera cornea* 1 hour and 20 minutes, for *Exidia albida* 1 hour and 15 minutes, and for *Dacryomyces deliquescens* 50 minutes.[1] These rapid rates of spore-development correspond to similar rapid rates for *Marasmius oreades* and *Collybia dryophila*, and appear to be correlated with the dependence of the fruit-bodies for their activity upon moist conditions. Rapid spore-development enables a dried fruit-body to resume its spore-producing function very quickly after the advent of rain.

In Chapter II, I showed by comparative observations that, on the whole, spores with walls which are warted or which are thick and pigmented take considerably longer to develop than spores with walls which are smooth and thin and colourless. Now the spores of the Tremellineae are all smooth and thin and colourless. There can be little doubt, therefore, that the simplicity of the spore-wall in this group is correlated with rapid spore-development.

We may connect up the ideas developed above as follows. The Tremellineae are lignicolous and therefore subjected to temporary periods of drought. They are therefore organised so as to retain their vitality when dry, and so as to resume their former shape and revive rapidly on the advent of rain. This organisation involves the production of a gelatinous matrix for absorbing and storing water rapidly and also involves the existence of basidia which ripen their spores in a minimum amount of time. The rapid ripening of the spores is favoured by the simplicity of the spore-walls, these being smooth and thin and colourless.

The forms of the fruit-bodies of the Tremellineae are very various. The most gelatinous fruit-bodies, *e.g.* those in the genera Dacryomyces, Tremella, and Ulocolla, consist of more or less spherical or hemispherical lumps which are either coarsely lobate or cerebriform at the surface (Fig. 56). In these, the hymenium covers the whole of the exterior surface. Part of, or the whole of, the hymenium, therefore, often *looks upwards*—a very exceptional

[1] *Vide supra*, Chapter II.

arrangement in the Hymenomycetes. Fruit-bodies with a less

FIG. 57.—*Hirneola auricula-judae*, a gelatinous fungus the fruit-bodies of which often somewhat resemble an ear in form. The wrinkled hymenial surfaces of the two fruit-bodies here shown looked downwards toward the earth. Photographed by A. E. Peck at Scarborough, England. Natural size.

gelatinous or more cartilaginous consistence, *i.e.* those which are most firmly built, tend to be so constructed that their hymenium

looks more or less *downwards*. This arrangement is seen, for instance, in *Auricularia mesenterica*, in *Hirneola auricula-judae*, and in *Femsjonia luteo-alba*. *Auricularia mesenterica* is broadly attached like *Stereum hirsutum* and has its hymenium confined to its lower surface. *Hirneola auricula-judae* (Fig. 57) is attached by a point and is ear-shaped. Its hymenium is limited to the concave surface of the ear ; and the ear, as it grows in size, gradually bends downwards so that the concavity is directed toward the earth. *Femsjonia luteo-alba* (Fig. 58) has small conical fruit-bodies which are reminiscent of the relatively gigantic hoof-shaped fruit-bodies of *Fomes fomentarius*. They grow downwards from the sides of fallen branches of Oaks and Birches and have a flattened under surface. This inferior surface is covered by the golden yellow hymenium, so that the basidia look more or less toward the centre of the earth. Among other gelatinous fungi in which the hymenium is restricted to the lower downward-looking surface of the fruit-body may be mentioned *Exidia glandulosa* (Witches' Butter), *Guepinia spathularia*, and *Tremellodon gelatinosum*, all of which I have studied in the woods around Kenora, Ontario. It is evident that many Tremellineae, but not all, respond to the stimulus of gravity in such a way as to cause the hymenium to look more or less downwards, thus resembling the more substantially constructed Agaricineae, Polyporeae, Hydneae, and Thelephoreae.

The fruit-bodies of the Tremellineae, with the exception of those which are more or less spherical or hemispherical, tend, as systematists have remarked, to resemble the fruit-bodies of the other main groups of the Hymenomycetes. Thus : (1) some gelatinous fruit-bodies form thin layers and are Corticum-like ; (2) *Auricularia mesenterica*, except for the slight wrinkling of its hymenium, resembles Stereum ; (3) Protomerulius, with pores on its under surface, resembles Merulius ; (4) Protohydnum and Tremellodon, with spines on their under surface, resemble Hydnum ; and (5) *Calocera cornea* and *C. viscosa* resemble unbranched and branched Clavariae respectively. A gelatinous fungus with obtuse, well-developed, gelatinous gills has recently been found in Africa, and Mr. C. G. Lloyd kindly sent me some specimens. Unfortunately, the fruit-bodies, when wetted, did not revive, and the basidia were

in such bad condition that I was unable to determine whether or not they were tremelloid in character.[1] The discovery of Tremellineae with gills cannot therefore be said to have been definitely made up to the present.

The basidia of the Tremellineae differ in structure from those of the Thelephoreae, the Clavarieae, the Agaricineae, the Polyporeae, and the Hydneae. Whereas in these five last-named groups of Hymenomycetes the basidia are clavate and unicellular, in the Auricularieae the basidia are elongated, cylindrical, and transversely septate; in the Tremelleae the basidia are more or less globose and divided into four cells by two crossing vertical partitions; and in the Dacryomyceteae the basidia have two long arms and are non-septate. The resemblance of various Tremellineae to Stereum, Merulius, Hydnum, Clavaria, etc., cannot therefore be due to direct inheritance, but must be accounted for by *phylogenetic convergence* taking place during the course of evolution. The Tremellineae discharge their spores in the same manner as the other Hymenomycetes and, in the struggle for existence, they have been compelled to adopt the same efficient forms for the production and liberation of their spores as we find in the Thelephoreae, the Polyporeae, the Hydneae, and the Clavarieae. The convergence in form which has come about by the fruit-bodies of the Tremellineae and of the non-tremelloid Hymenomycetes evolving along parallel lines finds many analogies elsewhere, among which may be mentioned (1) the convergence in dentition and habits of life of the metatherian mammalia of Australia and the eutherian mammalia of Europe, Asia, Africa, and North and South America, and (2) the development of cylindrical, so-called *telescope-eyes* by certain fishes, Crustaceans and Cephalopods which inhabit the depths of the sea.[2]

The basidia of the Tremellineae are somewhat different in form from those of the non-tremelloid Hymenomycetes, and this difference in form is doubtless accompanied by a corresponding

[1] C. G. Lloyd has named the fungus *Phyllotremella africana* and given some illustrations of it in his *Mycological Notes*, September 1920, p. 1007, and Figs 1850–1852.

[2] A Weismann, *The Evolution Theory*, translated by J. A. and M. R. Thomson, London, 1904, vol. ii, p. 323.

difference in physiological function. The various types of basidia in the Tremellineae will now be described, and I shall venture to make a few suggestions concerning their significance.

In the Auricularieae, the basidia are cylindrical, transversely

FIG. 58.—*Femsjonia luteo-alba.* Fruit-bodies growing downwards on a stick. In each fruit-body only the under surface is covered with a hymenium. Above, lateral view of stick in natural position. Below, same stick seen from below. Only the hymenial surfaces are now visible. Found at Tanworth-in-Arden, Warwickshire, England. Natural size.

septate, and four-celled ; each cell sends out a long sterigma which pierces through the gelatinous matrix ; and the whole of the protoplasm in each cell, except a very thin lining layer, passes into its associated spore. The basidia of most Uredineae are similar, except that they are curved instead of straight and project freely into the air instead of being developed in mucilage. The basidia

of Coleosporium, in being straight, transversely septate, and four-celled, and in having lateral sterigmata which pierce through mucilage derived from the walls of the basidia, are practically identical in their nature with those of Auricularia. There can be little doubt that the close resemblance of the basidia of the Uredineae and of the Auricularieae is based upon inheritance from a common ancestor. The septa in the long cylindrical basidia of the Auricularieae strengthen the basidia mechanically, and also serve to separate from one another the four masses of protoplasm which are destined to pass up the widely separated mouths of the sterigmata into the four spores. After separation from one another by the intervening septa, the four masses of protoplasm act as independent morphological and physiological units. This I take to be advantageous so far as spore-formation is concerned, owing to the distance of the mouths of the sterigmata from one another. It is probably simpler and easier for a long cylindrical basidium with lateral sterigmata to supply the proper amount of protoplasm to each of its four spores when it is septate than when it is non-septate.

In the Tremelleae, the basidia are more or less globular and are divided into four cells by two walls which cross one another at right angles through the basidium-axis.[1] Each of the four cells has a long arm or sterigma which pierces through the gelatinous matrix and comes to project into the air. By means of the crossing walls, the contents of each basidium, just as in the Auricularieae, are divided into four morphological and physiological units. Probably this division, especially since the basidium-body is globose, simplifies the work of supplying the proper amount of protoplasm to each spore. Now the non-tremelloid Hymenomycetes, *e.g.* the Agaricineae, have basidia which are clavate instead of globular and non-septate instead of septate, and which bear at their free ends four closely approximated relatively small sterigmata. No doubt the building of cross-walls in a basidium only takes place with the sacrifice of physiological energy and time as well as of organic substance. I therefore regard the basidia of

[1] It is possible that the septa in some species are not complete and that the four cells of the basidium open below into a common cavity.

the Agaricineae, since they have dispensed with cross-walls, as more highly evolved than those of the Tremelleae. The non-septation of the basidia of the Agaricineae, etc., seems to me much more wonderful and surprising than the septation of the basidia of the Tremelleae. For various reasons, both morphological and physiological, the septation of a basidium must be considered as a primitive condition and non-septation as a more highly evolved condition. In the Tremelleae the *globular* form of each basidium-body is made possible by the looseness of the hymenium, the individual basidia being surrounded by the gelatinous matrix and not pressing against one another. In the Agaricineae, etc., on the other hand, the *clavate* form of the basidium-body, with the four approximated end-standing sterigmata, is well suited to the compactness of the hymenium as a whole, for here the basidia and paraphyses are not isolated from one another but press against one another laterally. It may be that the original primitive septation of the basidia of the non-tremelloid fungi was eliminated as soon as, with the evolution of the compact hymenium, the basidia became clavate and came to have their four sterigmatic mouths placed close together. I am inclined to think that the approximation of the mouths of the sterigmata made it easier for the basidium to send up equal masses of protoplasm into the four spores and thus made possible and advantageous the elimination of the primitive septa.

In the Dacryomyceteae, the basidia are narrowly cylindrical and bifurcate at their ends into two long arms or sterigmata which pierce through the gelatinous matrix and develop their spores in free air. Here there is no septum dividing the basidium-body into two equal halves; and in the basidium-body being non-septate, the basidium of the Dacryomyceteae resembles that of the Agaricineae. I take it that the absence of a septum in the basidium of the Dacryomyceteae is correlated with the very narrowly cylindrical form of the basidium-body and the closely approximated sterigmatic mouths. The protoplasm of the basidium-body, in passing up into the sterigma, enters through two gates which are side by side. It is probably owing to these gates being so close to one another and thus the conditions for entry through both

being practically identical, that the basidium-body has succeeded in dispensing with the formation of a septum and thus with a preliminary division of its contents into two equal parts.

The hila of the spores of the Tremellineae are usually much more strongly developed than those of the spores of the non-tremelloid Hymenomycetes, such as the Agaricineae. Brefeld has shown this in his illustration of the basidia of Tremella, Dacryomyces, etc.; but he has always represented these hila as parts of the sterigmata pushing up past the ends of the spores.[1] This is incorrect. His supposed sterigmatic tips are really part and parcel of the spores and become detached with the spores when these are shot away from their sterigmata. This is well shown for *Calocera cornea* in Fig. 2 (p. 7), and for *Dacryomyces deliquescens* in Fig. 60, B. C.

The strong development of the hila of the spores of the Tremellineae is associated with a more violent discharge of the spores than occurs in most other Hymenomycetes. In violence of discharge, as measured by horizontal distance of discharge, the Tremellineae (excepting Calocera) are intermediate between the Uredineae and the non-tremelloid Hymenomycetes such as the Agaricineae and the Polyporeae. The following Table gives comparative statistics for spore-discharge. The measurements for the Uredineae were all made by Dietel,[2] except those for *Puccinia Malvacearum* and *Endophyllum Euphorbiae-sylvaticae* which were made by myself.

The methods used by me for determining the horizontal distance of spore-discharge in the Hymenomycetes were two. The first was to place the hymenium in a vertical plane in a closed compressor cell and then to observe with a horizontal microscope the distance from the hymenium at which the spores shot from their sterigmata first appeared when falling. The second was to place the hymenium

[1] O. Brefeld, *Untersuchungen*, Leipzig, 1888, Heft VII; *vide* for *Auricularia sambucina*, Taf. IV, Fig. 3; for *Exidia glandulosa* and *E. repanda*, Taf. V, Figs. 3 and 7; for *Tremella frondosa*, Taf. VII, Fig. 3; for *Dacryomyces deliquescens* and *D. stillatus*, Taf. IX, Fig. 2, and Taf. X, Fig. 13. Some of these illustrations are reproduced in F. von Tavel's *Vergleichende Morphologie der Pilze*, Jena, 1892, pp. 134, 141, 143, and 194.

[2] P. Dietel, "Über die Abschleuderung der Sporidien bei den Uredineen," *Mycologisches Centralblatt*, Bd. I, 1912, pp. 355-359.

in a vertical plane in a compressor cell as before, to wait until a spore-deposit had collected, and then, with a vertical microscope, to examine the preparation and measure the horizontal distance the spore-deposit extended away from the vertical plane of the hymenium.[1] The first method was used for the Polyporeae and Agaricineae and the second for the Clavarieae and Tremellineae. The special methods used for the Uredineae will be described in Volume IV.

Maximum Horizontal Distance of Spore-discharge in Basidiomycetes.

Group.	Subdivision.	Species.	Maximum horizontal Distance of Spore-discharge in Millimetres.
Uredineae	Coleosporiaceae	Coleosporium Petasitidis	0·6–0·85
		,, Campanulae	
	Pucciniaceae	Puccinia Malvacearum	0·6–0·85
		,, Glechomatis	0·6
		,, annularis	
	Endophyllaceae	Endophyllum Euphorbiae-sylvaticae	0·4–0·5
Tremellineae	Auricularieae	Hirneola auricula-judae	0·4–0·5
		Auricularia mesenterica	0·4–0·45
	Tremelleae	Exidia albida	0·4
	Dacryomyceteae	Dacryomyces deliquescens	0·5–0·65
		Calocera cornea	0·2
Non-tremelloid Hymenomycetes	Clavarieae	Clavaria formosa (sp. ?)	0·1–0·2
	Polyporeae	Polyporus squamosus	0·1
	Agaricineae	Amanitopsis vaginata	0·2
		Coprinus sterquilinus	
		,, curtus	0·1–0·12
		,, niveus	0·1
		Psalliota campestris	

The data embodied in the Table indicate that most of the Uredineae are able to shoot out their spores a horizontal distance of 0·6 mm., most of the Tremellineae 0·4 mm., and most of the non-tremelloid Hymenomycetes either 0·1 or 0·2 mm. Thus, so far as violence of spore-discharge is concerned, the Tremellineae (with the exception of Calocera), while holding an intermediate

[1] For these two methods *cf.* vol. i, 1909, pp. 135–142.

position, stand somewhat nearer to the Uredineae than to the non-tremelloid Hymenomycetes. This, perhaps, may be taken as one more small piece of evidence that the Tremellineae and the Uredineae are closely related.

It has already been pointed out that, under natural conditions, the whole or part of the hymenium of the most gelatinous fruit-bodies of the Tremellineae (Tremella, Ulocolla, Exidia, Dacryomyces, etc.) often looks more or less *upwards*. This upward-looking position is very exceptional in the Hymenomycetes and calls for some explanation in connection with the dispersal of the spores. In most Hymenomycetes, *e.g.* Stereum, Polyporus, Psalliota, and Hydnum, the hymenium is on the under surface of the pileus and always looks more or less downwards. This enables the spores, which are shot out from their sterigmata a distance of 0·1–0·2 mm., to fall into a space beneath the pileus and to be carried off therefrom by air-currents. If the hymenium were to look upwards, spores shot 0·1–0·2 mm. would be liable to fall back on the hymenium and adhere there before the wind could carry them off. The Discomycetes with upward-looking hymenia are successful in dispersing their spores because the spores are usually shot upwards from the asci for a distance not of 0·1–0·2 mm. but of 1–3 cm., *i.e.* about one hundred times farther than for most Hymenomycetes. This distance of discharge gives plenty of time for the wind to carry off the spores before they can fall back again on to the hymenium.[1] Now it is a remarkable fact that the gelatinous Hymenomycetes in which the whole or part of the hymenium looks more or less upwards discharge their spores much more violently than non-gelatinous Hymenomycetes in which the hymenium looks more or less downwards. It seems to me, therefore, that *the upward-looking position of the hymenium in so many Tremellineae and the exceptional violence of spore-discharge* in that group *are correlated*. We may conclude that, from the point of view of spore-dispersal, the disadvantage of the more or less upward-looking position of the hymenium of many Tremellineae, *e.g. Exidia albida* and *Dacryomyces deliquescens*, is compensated by extra violence in the discharge of the spores.

[1] *Cf.* vol. i, 1909, pp. 21–24.

In *Hirneola auricula-judae* and in *Auricularia mesenterica* the hymenium looks downwards and yet the violence of spore-discharge is some four or five times greater than from the hymenium of *Stereum hirsutum* and similar non-tremelloid Thelephoreae. The extra violence of discharge in the two Tremellineae appears to be unnecessary, but we can account for it as a primitive feature derived from ancestors in which the fruit-bodies were globose or lobate and the hymenium looked more or less upwards, which feature has been retained through inheritance although no longer of any especial use so far as spore-dispersion is concerned.

The fruit-bodies of *Calocera cornea* and *C. viscosa* have forms which are similar to those of unbranched and branched Clavariae respectively. It is noteworthy, therefore, that *Calocera cornea* and *Clavaria formosa* shoot off their spores with about equal violence (*cf.* the Table, p. 169). For the sake of convenience, a discussion of the relation of form to function in the fruit-bodies of Calocera will be deferred until we have become acquainted with this relation in Clavaria.

In the Tremellineae, just as in the non-tremelloid Hymenomycetes and in the Uredineae, a drop of water is excreted from the hilum of each spore just before discharge takes place. This was definitely observed for *Hirneola auricula-judae*, *Exidia albida*, *Dacryomyces deliquescens*, and *Calocera cornea*. In all these species the spores are elongated and have a curved axis, and in all of them the drop excreted at the hilum is about equal in diameter to the diameter of the spore (Fig. 2, p. 7). The drop begins to be excreted from the hilum about 5 seconds before the discharge of the spore in *Exidia albida*, about 10 seconds before in *Hirneola auricula-judae*, and about 16 seconds before in *Dacryomyces deliquescens*. The drop is always carried away by the spore when the latter is shot from its sterigma.

The Basidial and Oidial Fruit-bodies of Dacryomyces deliquescens.—*Dacryomyces deliquescens* (Fig. 59) is a very common fungus in England and appears during wet weather upon the surface of dead wood, such as old logs, rails, garden seats, gate-posts, etc.; but it was imperfectly described by the older systematists and by Massee, and its true nature is still misunderstood by many field

mycologists. Tulasne[1] studied its life-history and made the discovery (since confirmed by Brefeld[2]) that it produces two kinds of fruit-bodies which can be readily distinguished with the naked eye owing to colour differences: (1) orange fruit-bodies and (2) pale yellow fruit-bodies. Both are gelatinous. The orange fruit-bodies produce oidia and the yellow fruit-bodies basidiospores. The orange fruit-bodies were originally described as *Dacryomyces stillatus* Nees and the yellow fruit-bodies as *Dacryomyces deliquescens* Duby; and this erroneous division of one species into two is still generally retained in systematic handbooks. To clear up the confusion which has thus arisen, I shall now re-describe *Dacryomyces deliquescens* from my own observations.[3]

The orange fruit-bodies (Figs. 59, *o*, and 60, E, F) are rounded or hemispherical, 1–4 mm. in diameter and 1–2 mm. high, occurring in groups of more or less isolated individuals in lines along the grain of the woody substratum and often on its upper side so that they attract the eye. The yellow fruit-bodies are about the same size as the red ones, rounded, hemispherical or discoid, often somewhat wrinkled into folds at the surface especially where two or more fruit-bodies have anastomosed during development, and occurring like the red fruit-bodies in groups of more or less isolated individuals in lines along the grain of the woody substratum and often on its upper surface. In dry weather both the orange and the pale yellow fruit-bodies shrink very greatly, owing to loss of water, and become quite inconspicuous and difficult to find. When rain comes again, the fruit-bodies rapidly absorb water by imbibition and regain their former size and colour. There are few other fruit-bodies so dependent on atmospheric conditions as these.

In nature, the orange fruit-bodies often appear on the surface of wood in groups by themselves. The yellow fruit-bodies also often appear on the surface of wood in groups by themselves.

[1] L. R. Tulasne, "Observations sur l'organisation des Trémellinées," *Ann. des sci. nat., Bot.*, T. XIX, 1853, p. 211.

[2] O. Brefeld, *Untersuchungen*, Leipzig, 1888, pp. 141–152.

[3] This account of *Dacryomyces deliquescens*, except for the addition of illustrations, is identical with a paper called "The Basidial and Oidial Fruit-bodies of *Dacryomyces deliquescens*" which I published in *Trans. Brit. Myc. Soc.*, vol. vii, 1922, pp. 226–230.

Sometimes, however, patches of red and patches of yellow fruit-bodies appear near to one another on the same piece of wood but

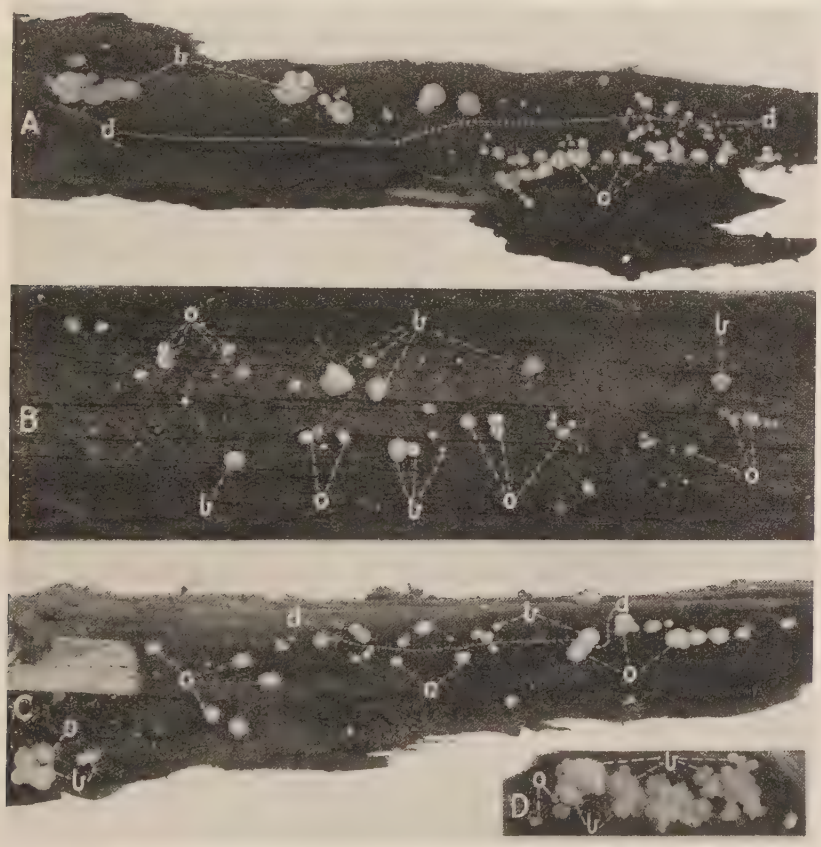


FIG. 59.—*Dacryomyces deliquescens*. Photographs showing yellow basidial and red oidial fruit-bodies on the same pieces of wood. A, soft wood (Larix ?); above the dividing line *d d* is a group of basidial fruit-bodies, *b*, and below it a group of oidial fruit-bodies, *o*. B, a piece of oak-wood bearing basidial fruit-bodies, *b*, mixed with oidial fruit-bodies, *o*. C, another piece of soft wood (Larix ?) bearing basidial fruit-bodies, *b*, above the dividing line *d d*, and oidial fruit-bodies below. To the left basidial and oidial fruit-bodies are mixed together. D, a piece of wood bearing a few small oidial fruit-bodies, *o*, and basidial fruit-bodies, *b*, which have become fused together into large gyrose masses during their development. Found at King's Heath, near Birmingham, England. Photographed natural size.

not intermingled; and, finally, sometimes red and yellow fruit-bodies appear on wood intermingled promiscuously. According to Tulasne, yellow fruit-bodies may be found which have red spots

upon them or which are gradually changing into red fruit-bodies.[1] The reason for these variations in the distribution of the two kinds of fruit-body under natural conditions is not yet understood, but the production of one kind of fruit-body rather than another doubtless depends on the physiological condition—possibly the nuclear state—of the underlying mycelium.[2]

An orange fruit-body (Figs. 59 and 60) has a gelatinous matrix derived from the swollen outer confluent hyphal walls, and this matrix, while firm toward its centre, is more and more readily deliquescent in wet weather as one passes toward its periphery. A fruit-body consists of two parts—an inner, firmer, paler core attached to the substratum, and an outer, more softly gelatinous, thick, bright orange, exterior coating. The core contains pale, thin, branched, anastomosing hyphae which run toward the periphery of the fruit-body and there thicken and give rise to branched chains of pale orange oidia (Fig. 60, E). Thus the thick orange outer coating of the fruit-body comes to be made up of oidia which are embedded in very soft jelly, and its colour is entirely due to the colour of the oidia. The oidia consist of one or two cells and show all stages of detachment from one another. Those on the very exterior of the fruit-body sometimes produce tiny conidia which project into the air. When rain comes, the outer part of the orange oidial zone deliquesces, *i.e.* the jelly absorbs so much water that it becomes liquid and flows. Thus during rain a large number of the outer oidia are washed away from the fruit-body and become dispersed. However, the production of oidia by the hyphae of the core is long continued so that new oidia gradually take the place of those previously washed away. It thus appears that the orange fruit-bodies are specialised for producing oidia and do not as a rule give rise to any basidiospores.

A yellow fruit-body, like a red one, has a softly gelatinous matrix derived from the swollen outer confluent hyphal walls. This matrix contains and envelops slender, branching, anastomosing hyphae which, toward the periphery of the fruit-body, branch

[1] L. R. Tulasne, *loc. cit.*, pp. 216–218, Pl. 13, fig. 2.

[2] *Cf.* P. A. Dangeard, "Mémoire sur la reproduction sexuelle des Basidiomycètes," *Le Botaniste*, T. IV, 1895, pp. 136–143.

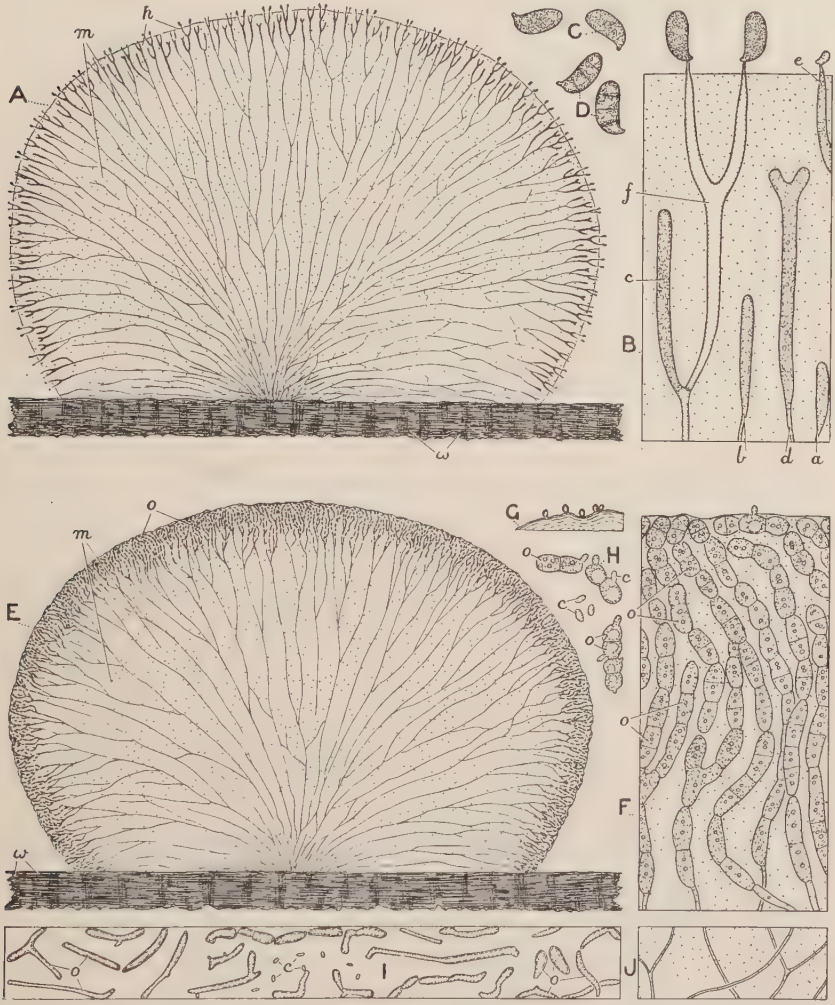


FIG. 60.—*Dacryomyces deliquescens.* A, semidiagrammatic vertical section through a small yellow fully expanded basidial fruit-body growing on a piece of wood, *w*, showing the hymenium, *h*, covering the exterior and the gelatinous matrix, *m*, penetrated by more or less radiating hyphae. B, a section through the hymenium showing basidia *a–f* in various stages of development. C, two spores which have just been shot away from their sterigmata. D, two spores which have been lying in water for a few hours and have become divided into four cells. E, semidiagrammatic vertical section through a red fully expanded oidial fruit-body growing on a piece of wood, *w*, showing the oidial layer, *o*, at the exterior and the gelatinous matrix, *m*, penetrated by more or less radiating hyphae. F, a section through the oidial layer showing the oidia, *o*, immersed in a gelatinous matrix. G, view of the surface of an oidial fruit-body showing a few conidia projecting beyond the gelatinous matrix. H, oidia, *o*, and conidia, *c*, found in a preparation made from an oidial layer. I, various oidia, *o*, and a few conidia, *c*, obtained in another preparation of an oidial layer. J, hyphae in the gelatinous matrix of an oidial fruit-body. Magnification : A and E, 30 ; B, C, D, F, G, H, 530 ; I, J, 220.

and rebranch to produce the basidia which make up the hymenium. Each basidium has a body which is slender and cylindrical and which develops at its apex two stout divergent arms or sterigmata, the tips of which come to penetrate through the surface of the gelatinous matrix (Fig. 60, B). Each sterigma produces at its free tip a single, elongated, curved spore which is provided with a well-marked hilum. The time taken for a spore to develop from a just recognisable rudiment to full size is only about 23 minutes. After a further 27 minutes the spore is discharged. Thus about 50 minutes only are taken up in the development, ripening, and discharge of each spore. There can be little doubt that this rapid rate of coming to maturity for each individual spore is a factor in assisting a revived fruit-body in rapidly resuming its spore-discharging function after rain. The drop excreted at the hilum begins to appear about 16 seconds before the spore is discharged, grows until it attains the diameter of the spore, and is then carried away by the spore when this is shot from its sterigma. A spore can be shot out from its sterigma 0·5–0·65 mm., so that although the hymenium often looks upwards, the wind has an opportunity of carrying away the spores before they can fall back on the hymenium.

Massee,[1] in his *British Fungus-Flora*, describes the yellow fruit-bodies of *Dacryomyces deliquescens* as follows.

"*Dacryomyces deliquescens* Duby.

"Gelatinous, rounded or irregular, convex, gyrose, yellow, hyaline, basal portion root-like and entering the matrix, spores cylindrical, obtuse, curved, 3-septate, 15–17 × 6–7 μ.

"*Dacryomyces deliquescens*. Duby, Bot. Gall., p. 729; Cke., Hdbk., p. 351.

"On pine-wood. In perfection during the winter months. Forming yellow subcircular convex masses 1–4 lines broad, often growing in long lines out of cracks in the wood."

Massee's statement that the spores are 3-septate is misleading. The fact is that the spores, when on their sterigmata and immediately after discharge, are *unicellular* just like those of other Tremellineae, and only become 3-septate and 4-celled when lying

[1] G. Massee, *British Fungus-Flora*, London, 1892, vol. i, p. 67.

in water and preparing to germinate. The spores of several other Tremellineae behave similarly.[1]

Massee says that the fruit-bodies occur on pine-wood. That is true, but my experience is that they occur on various kinds of wood both hard and soft, but especially on coniferous woods. Massee says that the fruit-bodies are 1–4 lines wide. These measurements seem to me a little too large. As Massee says, the fruit-bodies are yellow. However, I find that the fruit-bodies most exposed to the light are the yellowest, and that those which grow under logs and boards and in other very dark situations are relatively very pale yellow and sometimes almost colourless.

Massee,[2] in his *British Fungus-Flora*, describes the red fruit-bodies of *Dacryomyces deliquescens* as follows.

"*Dacryomyces stillatus* Nees.

"Gelatinous, rounded, convex, more or less plicate, persistently orange; spores cylindrical, curved, and multiseptate, 18–22 × 7–8 μ.

"*Dacryomyces stillatus*. Nees, Syst., p. 89, f. 90; Cke., Hdbk., p. 352.

"On pine and other decaying wood. Distinguished from *D. deliquescens* by its rather small size, firmer substance, deeper orange colour, and larger, multiseptate spores. Usually barren."

Massee describes these red fruit-bodies as being more or less plicate. My experience is that they are mostly hemispherical and irregularly humped or obtusely tuberculate rather than plicate. He also says: "Spores cylindrical, curved, multiseptate, 18–22 × 7–8 μ," but he fails to tell his readers that by "spores" he means not basidiospores, but *oidia* embedded in the gelatinous outer layer of the fruit-body. Each oidium has at least one septum across it, but the oidia hang together in chains and show all

[1] In his illustration of a basidium of *Dacryopsis nuda* Mass. in his *British Fungus-Flora* (vol. i, p. 56), Massee represents the spores on the sterigmata as 3-septate and 4-celled. It is not unlikely that this is an error and that the spores on the sterigmata should have been represented as unicellular. Massee may have found isolated spores lying on the hymenium which had become 3-septate after discharge and have then supposed that they were 3-septate before discharge.

[2] G. Massee, *loc. cit.*, p. 67.

stages of separation from one another. Only the chains of oidia are multiseptate. The width of the oidia I find to be 2–4 μ and not 7–8 μ. They are but rarely as wide as the basidiospores. The two-celled oidia are 12–15 μ long, but chains of these oidia imperfectly separated from one another may be 45 or even 60 μ long. The oidia are usually curved or undulate and are sometimes more or less **Y**-shaped. In each cell there are usually two small central rounded bright spots, so that the chains of cells are guttulate. The oidia on the exterior of the fruit-body produce a few tiny oval conidia about 2 μ long. If a red fruit-body be touched into a drop of water on a slide, some of these conidia can usually be found in the drop among the oidia, and occasionally one may find them attached to their oidia. Massee says that the fruit-bodies are "usually barren." Exactly what is meant by this is not clear. As a matter of fact the red fruit-bodies always produce a crop of oidia and never any basidiospores.

A brief description of *Dacryomyces deliquescens*, suited for systematic purposes, is as follows:

DACRYOMYCES DELIQUESCENS Duby.

Synonym for the oidial stage: *Dacryomyces stillatus* Nees.

Basidial fruit-body—gelatinous, convex, rounded, or irregular when confluent, often slightly plicate or gyrose, yellow, translucent, 1–6 mm. in diameter, basal portion emerging from the wood at the central point. Basidiospores cylindrical, curved, obtuse, 12–15 $\times$ 5–6 μ, one-celled when discharged from the sterigmata but after lying in water soon becoming triseptate and four-celled.

Oidial fruit-body—gelatinous, convex, mostly hemispherical, not plicate, but when large often irregularly humped up at the surface, bright orange, rather opaque, 1–3 mm. in diameter, basal portion as before. Basidiospores never present. Oidia very numerous, embedded in the outer gelatinous layer which deliquesces in rainy weather and sets them free, formed in branching chains, cylindrical, curved or flexuose, sometimes forked, usually two-celled but forming chains owing to imperfect separation, width

2–4 μ, length when two-celled 12–15 μ, but forming chains up to 60 μ long, sometimes bearing one or two minute oval conidia 2μ long, contents pale orange with one or two clear guttules in each cell.

Lignicolous, occurring on many different kinds of wood, especially coniferous woods. Common everywhere, often seen in gardens on old pine boards, wooden rails, arbour-work, etc. It is to be found all the year round but is conspicuous only in wet weather. The two forms of fruit-bodies were originally described by Duby and Nees as independent species and have always been so treated by systematists, the basidial form being called *Dacryomyces deliquescens* and the oidial form *D. stillatus*; but Brefeld has proved that they are nothing but two stages of the same species. They may be found separated from one another on different substrata, or in separate patches side by side on the same substratum, or occasionally intermingled. According to Tulasne some of the yellow fruit-bodies may at times be marked with red patches of the same nature as the red fruit-bodies.

Spore-discharge in the Clavarieae. - In the genus Clavaria, the sporophore is usually erect, and either simple and club-shaped or variously branched. The forms of the fruit-bodies in Clavaria, just as in the Agaricineae, the Polyporeae, and the Hydneae, are significant in respect to the efficiency of the fruit-bodies in producing and liberating spores.

The hymenium in Clavaria is borne upon the exterior surface of the sporophore, and the erect more or less narrowly club-shaped or much-branched cylindrical forms of the fruit-bodies evidently serve to provide a considerable amount of hymenial surface relatively to the fruit-body mass. A simple, solid, erect, basally supported, more or less cylindrical, terminal *branch* of a branched Clavaria corresponds to a simple, hollow, vertical, more or less cylindrical, hanging *tube* of a Polyporus or Boletus. In both, the hymenium is a thin more or less cylindrical layer, but in the Clavaria the solid supporting flesh is within the cylinder and the hymenium looks outwards, whereas in the Polyporus or Boletus the solid supporting flesh is outside the cylinder and the hymenium looks inwards. The cylinders of hymenium are produced successfully

on far less massive fruit-bodies in a Clavaria than in a Polyporus or Boletus but, owing to their mode of support, it is impossible for them to be so fine and numerous in a Clavaria as in a Polyporus or Boletus. Hence, in a Clavaria, although the form is very simple and obviates the production of a thick pileus-flesh, the simplicity and the saving of flesh are accompanied by the production of a comparatively limited hymenial area. Moreover, in a Clavaria,

FIG. 61.—*Clavaria pistillaris*. The fruit-body has a simple club-shaped form and typically takes up an upright position. The fruit-bodies here shown have been somewhat damaged and disturbed by a rodent. Photographed in the Wienerwald, near Vienna, by Somerville Hastings. Natural size.

the hymenium is directly exposed to the sun and air and is therefore much more liable to suffer from the effects of dry or rainy weather than the hymenium of a Polyporus or Boletus. As judged by number of species and frequency of occurrence, the Clavarieae as a group are much less successful than the Polyporeae and the Agaricineae. In all probability this is due, in part at least, to the relatively small amount of hymenium and therefore to the relatively small number of spores produced by even the largest fruit-bodies, and also to the hymenium being exposed on the surface of the fruit-body instead of being protected by being disposed upon gills or in tubes on the under side of the fruit-body.

Clavaria pistillaris, which I have seen growing at Kenora on the Lake of the Woods, is one of the simplest and at the same time one of the largest species of Clavaria (Fig. 61). It resembles an upright club and grows to a height of from 4 inches to 1 foot. The shape of the fruit-body and the upright position which it assumes ensures that the hymenium, just like that of *Craterellus cornucopioides*, shall look downwards toward the earth. The obconic form of the fruit-body is undoubtedly favourable to spore-discharge, for the spores, on being shot from the hymenium on the sides of the fruit-body, fall into a space from which they can be easily carried away by the wind. I suspect, as a result of observations made on other smaller species, that there is no hymenium at all on the top of the fruit-body, but up to the present I have had no opportunity of deciding this point by direct investigation.

An obconic form of the fruit-body, which enables the hymenium to look more or less downwards toward the earth, while especially noticeable in the relatively gigantic *Clavaria pistillaris*, is also characteristic for *Clavaria ligula*, *C. fistulosa*, *C. vermicularis*, *C. rosea*, and other unbranched species of Clavaria, as well as for the species included in the genus Pistillaria. A certain saving of fruit-body substance is effected in *Clavaria pistillaris* by the flesh being loose and cottony in the centre instead of being solid, and in *C. fistulosa* by the clubs becoming hollow with age.

The simple clavate fruit-bodies of *Clavaria vermicularis* (Fig. 62) and *C. rosea* are not entirely covered with a hymenium, for I have found that no spores whatever are produced either upon their lower, thinner, stalk-like bases or at their apices. In these species, and doubtless generally in others resembling them, the hymenial layer has the form of a more or less vertical hollow cylinder which gradually diminishes in thickness from above downwards. When the axis of a clavate fruit-body is exactly vertical, therefore, the hymenium looks more or less downwards, an arrangement which, as in the gills of the Agaricineae, the tubes of the Polyporeae, and the spines of the Hydneae, favours the liberation of the spores and their dispersion by the wind. When, however, as often happens, the axis of a clavate fruit-body is not quite vertical but is inclined

from the vertical at some angle, *e.g.* 15°, part of the hymenium instead of looking slightly downwards or being vertical, looks slightly upwards. This upward-looking position of part of the hymenium, however, is not so fatal for spore-dissemination as in the Agaricineae or Polyporeae because the hymenium is well exposed to the wind. It is probable that, when a spore has been

Fig. 62.—*Clavaria vermicularis*. Cylindrical fruit-bodies coming up among grass in October at Haslemere, England. Photographed by Miss E. M. Wakefield. Natural size.

shot away from its sterigma on the upper side of an inclined fruit-body, air-currents sweeping round the fruit-body carry the spore away before it has time to fall back on to the hymenium.

Let us now consider the form of such a branched Clavaria as *Clavaria pyxidata* (Fig. 63). The fruit-body is seated on the ground, is negatively geotropic, and therefore erect. The main stem which probably is always barren is produced first. This branches and rebranches so that, as we proceed upwards, the branches become finer and finer. The upper branches are fertile and produce spores. It is to be especially noted that the upper spore-producing branches, although becoming ever thinner as we

proceed basifugally, are all more or less *obconic*, *i.e.* have the same general form as the simple club of *Clavaria pistillaris*. A branched Clavaria is, therefore, in many species at least, nothing but a compound club (*cf.* Fig. 64). Thus, in *Clavaria pyxidata*, the branches belonging to the three last branch-systems—all of which are spore-bearing—are all narrowest at their base and gradually thicken toward their tops; and each branch which rebranches produces at its expanded top two or more narrowly-based still thinner branches. We have here, as it were in miniature, the fruit-body of a *Clavaria pistillaris* which, instead of ending bluntly, branches at its top and produces there a limited number of new and smaller clubs which in their turn rebranch and produce still more new and yet smaller clubs.

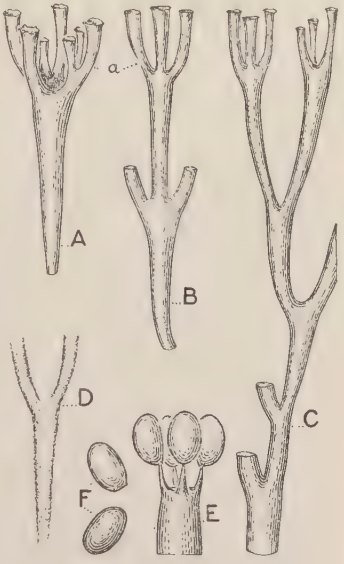


FIG. 63.—*Clavaria pyxidata*. A, B, and C, branches of a fruit-body composed of obconic elements, the terminal elements *a* being hollowed at the top like the podetia of the lichen *Cladonia pyxidata*. Since the branches have an upright habit, the hymenium which covers them looks more or less downwards. D, a spore-deposit from a forked branch. E, the upper part of a basidium showing the sterigmata and spores. F, two spores from a spore-deposit. Drawn from a fruit-body collected by Rudolf Hiebert at Gimli, Lake Winnipeg. A, B, C, and D, enlarged to $1\frac{1}{3}$. E, and F, magnification 1,414.

It was remarked above that the basal parts of branched Clavariae are probably always barren. Such barrenness I actually observed in mature fruit-bodies of *Clavaria pyxidata*, *C. formosa*, and *C. cinerea*. The absence of a hymenium from the basal parts of these fruit-bodies was proved by studying the surface with the microscope and by the non-production of spore-deposits. When a fruit-body was laid horizontally in a small chamber in which it could transpire but very slowly, the upper halves of the fruit-bodies alone produced spore-deposits and the basal parts no deposits whatever. We thus find that only those parts of the fruit-bodies produce spores which project above the substratum most

freely, and which therefore have the best chance of liberating their spores so that these may be carried off by the wind.

It is true that the upper branches of branched Clavariae are not truly vertical throughout but only more or less so ; but it must be granted that the hymenium for the most part looks slightly downwards or horizontally rather than slightly upwards. This general position of the hymenium is distinctly advantageous for the liberation of the spores and corresponds to what we find for the hymenium in the Agaricineae, the Polyporeae, and the Hydneae.

Fig. 64. —*Clavaria* (*abietina* ?), a branched fruit-body with an upright habit. Each larger branch has the form of a compound club. Photographed at Scarborough, England, by A. E. Peck. Natural size.

That part of the surface of compound Clavariae, *e.g. Clavaria pyxidata* and *C. formosa*, which looks most directly upwards, *i.e.* the upper sides of the forks where branching takes place and the tips of the ultimate branches, never produces any hymenium or spores. Of this I have been able to convince myself by repeated observation with the microscope and by the study of the position of spore-deposits. Upon examining a spore-deposit obtained by laying a piece of a compound Clavaria flat on a glass slide in a closed chamber, I always found that no spores had been deposited by the surface layers of the fruit-body situated on the upper side of the forks or covering the free tips of the ultimate branches, but that spore-deposits had been yielded by all those surface layers which, before the fruit-body had been gathered, had been vertically situated or had looked more or less downwards. It is possible that the non-production of a hymenium in the forks of the branches is due to a regulating stimulus of gravity. Such a stimulus decides in *Sparassis crispa* that the hymenium shall be developed only on

those parts of the ultimate branches which look more or less downwards and never on those parts which look more or less upwards [1]; and the same kind of stimulus may be more or less effective in Clavaria. Here again there is room for an experimental investigation.

The upper angles between the branches in many species of Clavaria are very obtuse or rounded out. This causes a marked separation of the branches at their bases and enables the main shafts of the branches to grow upright with a minimum of mutual interference. In such species, also, the inter-ramal spaces are well developed. This increases the ease with which the wind may sweep through the fruit-body and carry away the spores. In some species, *e.g. Clavaria pyxidata*, the branches, when they happen to grow toward one another and press against one another, fuse at the points of contact. This enables the fusing branches to act as a unit in rebranching, instead of independently, and at the same time strengthens the fruit-body mechanically.

The basidia of the Clavariae are unicellular and have four sterigmata and four spores, and they therefore resemble the basidia of the Agaricineae and other non-tremelloid Hymenomycetes. The spores are discharged in the usual manner, *i.e.* violently and after a drop of watery fluid has been excreted at the hilum. I observed spore-discharge with the microscope more particularly in *Clavaria formosa*. A subterminal branch bearing several terminal branches was placed in a closed compressor cell; but, under these conditions, the basidia ceased to discharge their spores properly and the cover-glass became fogged. I therefore laid a similar piece of the fungus on an ordinary glass slide and covered it with the cap of a large compressor cell. As this cap was greater in diameter than the width of the slide, ventilation spaces were left open below on each side of the slide. Under these conditions there was no fogging of the cover-glass of the cell cap and the basidia behaved normally. Shortly before a spore was to be discharged, a drop began to be excreted at the spore-hilum. As soon as this drop had grown for about five seconds and had attained a diameter equal to about three-quarters or the whole of the diameter of the spore, the spore

[1] *Vide infra.*

was discharged. The spore and drop were shot away from the sterigma together, the spore doubtless with the drop clinging to it as in other Hymenomycetes. The four spores of each basidium were discharged successively in the course of a few minutes.

The horizontal distance to which the spores were discharged before falling vertically in still air was found by measuring the horizontal distance to which spore-deposits extended away from the sides of branches laid flat in a large compressor cell. The maximum horizontal distance of spore-discharge was thus found to be 0·1–0·2 mm. This observation tends to show that, in Clavaria, the violence of spore-discharge is equal to, but no greater than, that of the other non-tremelloid Hymenomycetes. The discharge of the spores from the hymenium a horizontal distance of 0·1–0·2 mm. must aid the spores in being carried away by the wind as it sweeps through the inter-ramal spaces of the fruit-body.

In the foregoing part of this section, our chief consideration has been with Clavaria. A few words may now be added concerning other genera of Clavarieae.

Pistillaria resembles an unbranched Clavaria in form, but the clubs occur on dead thistles, grass-stems, leaves, etc., are minute and become rigid when dry. The clubs are either sessile or attenuated downwards into a continuous stem-like base which is not distinctly defined. Doubtless what has been said about the unbranched Clavariae in respect to form and function very generally applies to Pistillaria.

In Typhula which is usually unbranched, the fertile part of the fruit-body is cylindrical and rarely clavate, and it is raised above the substratum of fallen leaves, etc., by means of a distinct filiform sterile stem. In the upper part of the fruit-body being specialised for the production of spores and the lower part being sterile and specialised for raising the upper fertile part to some distance above the substratum, we have an interesting division of labour which finds exact parallels in the sporophores of the pyrenomycetous genera Claviceps and Cordiceps and in the discomycetous genus Geoglossum. The cylindrical rather than clavate form of the fertile portion of Typhula is remarkable ; but this portion is usually very decidedly negatively geotropic so that its hymenium is almost

vertically situated. Doubtless, owing to the vertical position of the hymenium, the narrowness of the cylinders which the hymenium covers, and the solitariness of the fruit-bodies, the wind is given ample opportunity to carry away the discharged spores.

In Pterula, the fruit-bodies are mostly branched. The branches are filiform and in some species, *e.g. Pterula subulata*, fuse where they touch. Here, as elsewhere, union is strength and the fusion of the component parts of the fruit-body to some extent compensates for their individual weakness. The hymenium is said to cover the surfaces of the branches, but as yet I have not had an opportunity to verify this statement. Pterula, in having filiform branches, has reached the extreme limit of the Clavaria type of organisation. Owing to the fineness of its branches, it provides far more surface area per unit of fruit-body mass for the development of the hymenium than any of the other genera of Clavarieae. As if to compensate for the fineness of the branches, the flesh of the Pterulae is stiff and cartilaginous. It may be that species of Pterula retain their vitality when dried and revive in wet weather, in this way differing from the soft-fleshed species of Clavaria ; but of this, up to the present, experimental evidence is lacking.

According to Patouillard,[1] the genus Pterula contains about twenty species, some of which have their branches slightly compressed and the hymenium unilateral. Doubtless, the hymenium, when unilateral, is on the under side of the flattened branches and not on the upper side. These species of Pterula with slightly flattened branches are of especial interest from the point of view of evolution. In Pterula the branches in most species are so fine that they have some difficulty in supporting themselves in a strictly vertical position and are therefore more or less inclined, with the result that part of the hymenium looks more or less upwards. As a reaction against this inconvenience, which has arisen from pushing the Clavaria type of organisation to its extreme limit, some of the species have become thelephoraceous, *i.e.* have developed branches which are slightly flattened and dorsiventral with the hymenium restricted to the under surface only.

[1] N. Patouillard, *Essai taxonomique sur les Familles et les Genres des Hyménomycètes*, Lons-le-Saunier, 1900, p. 42.

Sparassis (Fig. 65) was placed by Patouillard and most systematists in the Clavarieae because it was believed that the hymenium was amphigenous, but Cotton has now shown that the hymenium is limited to the lower sides of all the branches, however wavy their form may be. Cotton therefore holds the view, with which I agree, that Sparassis must be removed from Clavarieae

Fig. 65.—Sparassis. Upper part of a fruit-body, four and one-half inches across. On the left-hand side, the specimen has the characters of *S. crispa* and, on the right-hand side, those of *S. laminosa*. Photographed by Miss E. M. Wakefield at Woking, England. Natural width reduced by one-quarter of an inch.

and be placed in the Thelephoreae near Stereum.[1] There can be little doubt that the dorsiventrality of every part of each curled branch of Sparassis is brought about by the stimulus of gravity, and that the resulting ventrality of the hymenium is advantageous for the dissemination of the spores.[2]

Some observations of my own on the position of the hymenium in *Sparassis crispa*, which confirm and extend those of Cotton,

[1] A. D. Cotton, "On the Structure and Systematic Position of Sparassis," *Transactions of the British Mycological Society*, vol. iii, 1912, pp. 333–339.

[2] *Cf.* A. H. R. Buller, *Researches on Fungi*, vol. i, 1909, pp. 21–24.

may here be described. A fruit-body, which was 10 inches long and still developing, was found by Mr. W. B. Brierley at the foot of a Scots Pine (*Pinus sylvestris*). He gathered it and at once kindly brought it to me at the Herbarium at Kew, where I happened to be working. On examining the laminae upon the head of the fruit-body, I found that the layers of hymenium were situated always on the lower sides of the folds, and never on the upper. The position of the hymenium, as seen in vertical sections, is indicated by thicker lines in such positions as *h* in the drawings B, C, and D of Fig. 67. I then took the fruit-body and suspended it in a glass case which had been used as a microscope cover (Fig. 66). The already-mentioned hymenial layers now looked downwards. Under these conditions the edges of the terminal laminae continued to develop in area. After the lapse of two days these young and terminal laminae were found to have developed basidia on their lower sides, but not on their upper. Thus, while the old layers of hymenium, which had been developed under natural conditions, now looked upwards, the new layers of hymenium, which had developed on the fruit-body after its inversion, now looked downwards. This experiment shows that, by inverting a young fruit-body, one can at will invert the position

FIG. 66.—*Sparassis crispa*. Effect of gravity on the position of the hymenium. A fruit-body was suspended by its stipe in an inverted position in a glass case, as here shown. The ends of the fronds continued to grow. The new hymenial layers developed only on the sides of the fronds which happened to face toward the base of the case and away from the stipe. About $\frac{1}{5}$ natural size.

of development of the hymenium ; and it also clearly demonstrates that the laminae owe their dorsiventrality'—their sterility on their upper surfaces and their fertility on their lower surfaces—to the stimulus of gravity.

It is quite possible that Sparassis, although now developing like a compound Stereum, was originally derived from a Clavaria, for it arises from the ground on a central stem, branches and re-branches like many branched Clavariae, and has soft Clavaria-like flesh. We have only to suppose that the original erect, radial,

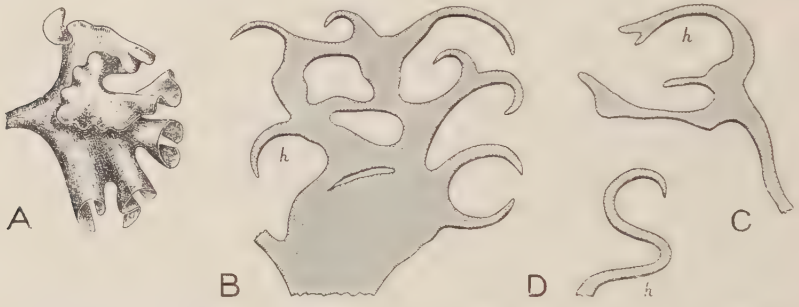


FIG. 67.—*Sparassis crispa.* Position of the hymenium. A, one of the terminal fronds of a large fruit-body showing its naturally curled condition. B, C, and D, vertical sections through parts of a fruit-body. The blacker lower lines, *h h*, represent the hymenium which always looks downwards. B shows anastomoses of fronds. D is an S-shaped frond with the hymenium on the lower side of each ascending part. Natural size.

fertile branches, covered with cylindrical layers of hymenium, became drooping, flattened, and at the same time responsive to a morphogenic stimulus of gravity, which caused them to become dorsiventral with a barren upper side and a fertile under side. The general habit and the nature of the flesh therefore suggest that Sparassis may have become thelephoraceous rather by convergence than by direct descent. The view that such an approach to the Thelephoreae may have taken place in the course of evolution is supported also by the fact that in certain species of Pterula, to which reference has already been made above, the branches have become slightly compressed and also dorsiventral, the hymenium being restricted as in true Thelephoreae to the ventral surface only.

The Genus Calocera.—This genus, in accordance with the

classification given at the beginning of this Chapter, is included in the Tremellineae. The fruit-bodies of Calocera resemble those of Clavaria very closely in form ; and there are few beginners in mycology who, on first finding such a species as *Calocera viscosa*, do not mistake it for a Clavaria. Unbranched species of Calocera, *e.g. C. cornea*, correspond to unbranched Clavariae, and branched

FIG. 68.—*Calocera cornea*, yellow gelatinous fruit-bodies growing at the base of a tree. Photographed in a wood at Oxshott, Surrey, England, by Somerville Hastings. Natural size.

species, *e.g. C. viscosa*, to branched Clavariae. Calocera differs from Clavaria, however, in that it is subgelatinous, becomes horny on drying, revives in wet weather after having been dried, and in that its basidia possess a distinctive form. The basidium of Calocera, instead of being clavate and bearing four slender sterigmata and as many spores, is cylindrical and bifurcated into two long and thick arms or sterigmata which penetrate the gelatinous matrix, just as in a Tremella, and bear aerially one spore each.

The fruit-bodies of *Calocera cornea* (Fig. 68) are often found growing out from the sides and tops of old logs, tree stumps, etc. They are slenderly clavate in form and usually unbranched. Just

as in the unbranched Clavariae, the lower more stalk-like part of each club and the club apex are barren, the hymenium covering only that part of the club which lies between these two regions. The fruit-bodies, when growing out from the side of a stump, do not turn upwards very readily and, doubtless, are not strongly negatively geotropic. Whether or not the upper sides of more or less horizontal clubs produce basidia and basidiospores remains to be investigated. A spore of *Calocera cornea*, as recorded in Chapter I, was found to develop from a just visible tiny rudiment to full size in 40 minutes and to be discharged at the end of another 40 minutes, discharge being preceded by a drop-excretion at the spore-hilum (Fig. 2, p. 7). A sterigma which has produced a spore collapses a few minutes after the spore has been discharged, and never produces a second spore.

The horizontal distance of spore-discharge in *Calocera cornea* was found by laying a fruit-body, which had been revived after drying, in a closed compressor cell, waiting until a spore-deposit had accumulated, and then measuring with the microscope the horizontal distance from the sides of the fruit-body to which the spore-deposit extended. This distance was found to be 0·2 mm. although most of the spores were found to have settled about 0·1 mm. from the fruit-body. From this observation we can conclude that the violence of spore-discharge in *Calocera cornea* is not nearly so great as in other Tremellineae such as *Hirneola auricula-judae*, *Auricularia mesenterica*, *Exidia albida*, and *Dacryomyces deliquescens*, but is about equal to that of *Clavaria formosa*. For comparative data upon the violence of spore-discharge the reader is referred to the Table on p. 169.

Calocera viscosa has a bright orange-yellow fruit-body which forks once or twice upwards. The terminal branches of a fruit-body are very erect, but are rather cylindrical than clavate and taper to a point. I found by studying the position of spore-deposits yielded by mature fruit-bodies in still air in small closed chambers that, just as in certain branched Clavariae, the hymenium does not cover the whole surface of each fruit-body but is lacking in the lower portions of the fruit-bodies, at the apices of the terminal branches, and on the upper side of each fork.

From the foregoing observations it appears that the relation of general form to function is practically identical in Calocera and Clavaria.

Spore-discharge in the Exobasidieae.—The Exobasidieae are parasitic in the tissues of living Flowering Plants, produce no special fruit-bodies, and develop their hymenia on the epidermis of their hosts. They thus correspond to the Exoascaceae. Two genera only have been recognised as belonging to the Exobasidieae, namely, Exobasidium with about twenty species and Microstroma with two.[1]

The Exobasidieae differ from the other groups of Hymenomycetes in the non-production of a fruit-body. The function of a fruit-body from the mechanical point of view is twofold: to produce an extended surface upon which the hymenium can be developed and to place that surface in such a position that the spores, as soon as they are shot from their sterigmata, may be carried off by the wind. These ends in the Agaricineae, the Polyporeae, etc., are secured only by the construction of a considerable amount of fruit-body substance. Now, in the Exobasidieae, the production of a fruit-body would be superfluous, owing to the fact that the host-plant provides the parasite with a surface upon which the hymenium can be developed and which is favourably situated for the dispersion of the spores. It is very probable that the Exobasidieae had saprophytic ancestors which produced their hymenia on fruit-bodies but that, after the fungi became parasitic, these fruit-bodies underwent gradual elimination.

Exobasidium Vaccinii occurs on the living leaves of various species of Vaccinium. I myself have seen it in Yorkshire on the leaves of *Vaccinium Myrtillus*. It causes hypertrophy in the leaves which it infects, so that they bulge outwards in a bladder-like manner on their under surfaces. The surface of each of these hypophyllous galls is covered with a flesh-coloured hymenium. The hymenium, being thus placed on the lower side of each infected leaf, looks more or less downwards in the same manner as the hymenium of the Agaricineae, Polyporeae, etc. This position is very favourable for spore-dispersal, for there is a space below it from which the wind may carry away the falling spores. The

[1] Engler und Prantl, *Die nat. Pflanzenfamilien*, Teil I, pp. 103–105.

position of the hymenium in Exobasidium may be decided not by the stimulus of gravity but by the structure of the leaf of the host. The gall serves to increase the amount of surface which the hymenium can occupy and thus favours the production of a larger number of spores.

A Brazilian species of Exobasidium, *E. Leucothoës*, according to Hennings,[1] causes galls on the twigs of Leucothoë, which resemble witches' brooms or the branches of a Clavaria. Thus a special new surface area of considerable extent comes into existence upon the host upon which the hymenium can be deployed. We thus see that here, as in *E. Vaccinii*, the parasite moulds its host, in much the same manner as do many insects, into forms which are favourable to its own existence.

[1] P. Hennings, in Engler u. Prantl, *loc. cit.*

CHAPTER VII

THE RED SQUIRREL OF NORTH AMERICA AS A MYCOPHAGIST

Introduction—Squirrels Observed Eating Fungi—Winter Stores of Fungi—Storage in Bulk—Storage in the Forked Branches of Trees—The Storage of Fungi in Relation to Climate—Two Chickens Hung in a Tree—Summary

Introduction.—In the *Transactions of the British Mycological Society* for 1916, an interesting paper was published by Hastings and Mottram upon the edibility of fungi for rodents. It was shown by citations from other authors, by field observations, and by a series of experiments, that both squirrels and rabbits attack the fruit-bodies of many of the higher fungi and devour them as food.[1] Two of their illustrations are here reproduced. The first (Fig. 69) shows the upper surfaces of two *Boletus badius* fruit-bodies which have evidently had their pileus-flesh gnawed down to the tops of the hymenial tubes by some rodent. The tooth-marks are exactly like those made by rabbits on fungi under experimental conditions, and we may therefore conclude that the damage was done by these animals. The second illustration (Fig. 70) shows some of the subterranean fruit-bodies of *Elaphomyces granulatus*. The right-hand fruit-body, which had been partly devoured, was found at the surface of the ground in Oxshott Woods, Surrey. As indicated by the tooth-marks, it had been unearthed by a rodent, in all probability by a squirrel. Squirrels are attracted to the fruit-bodies by their smell and dig down in the forest mould until they find them.

The investigations of Hastings and Mottram were made in England, but their conclusion that squirrels and rabbits are mycophagists doubtless applies not merely to British species but

[1] S. Hastings and J. C. Mottram, "The Edibility of Fungi for Rodents," *Trans. Brit. Myc. Soc.*, vol. v, 1916, pp. 364–378.

very generally to non-British species the world over. As a contribution to our knowledge of the relations of rodents and fungi

FIG. 69.—*Boletus badius* fruit-bodies eaten by rodents, presumably rabbits. The pileus-flesh, which has been gnawed down to the top of the hymenial tube-layer, shows tooth-marks like those made by rabbits. Found in Oxshott Woods, Surrey, England, and photographed by Somerville Hastings. Natural size.

I shall here record a series of observations upon the Red Squirrel and its fungus food, made by myself and by several other naturalists in Canada and the United States.[1]

The Red Squirrel or Chickaree, *Sciurus hudsonicus* (Figs. 71 and 72), has an extensive geographical range in North America, for it is found in the woods of Canada and the northern part of the United States from the east coast to the Rocky Mountains.[2] It does not hibernate profoundly during the winter, for on any sunny winter's day it may be seen about the trees in woods.[3] I myself have seen it in mid-winter at Winnipeg in a park and about houses. The Red Squirrel feeds on the seeds of fir cones, nuts, etc., but it is also an habitual mycophagist. In the autumn, it often collects fleshy fungi in large numbers for its winter supply of food, and it stores the fungi sometimes in holes and sometimes on the branches of trees. This latter mode of storage, although of peculiar interest, does not seem to be generally known to mycologists even in North America.

Squirrels Observed Eating Fungi.—Whilst studying fungi in the woods at Gimli on the western shore of Lake Winnipeg, at Minaki on the Winnipeg River, and at Kenora on the Lake of the Woods, I have many times observed fruit-bodies of Hymenomycetes which had been partly devoured or otherwise injured by rodents. From the appearance of the damaged fungi, which was similar to that described by Hastings and Mottram, I came to the conclusion that the destructive agent was sometimes a squirrel and sometimes a rabbit.

In the autumn of 1919, I spent many days studying the fungi in the woods about Kenora. There, in the first week of October, *Armillaria mellea*—the Honey Fungus—was exceedingly common (Fig. 73), and I noticed that, here and there, clumps of it had been damaged by a rodent. I also found a few isolated, half-eaten fruit-bodies hanging in the forks of branches of trees at a height

[1] *Cf.* A. H. R. Buller, "The Red Squirrel of North America as a Mycophagist," *Trans. Brit. Myc. Soc.*, vol. vi, 1920, pp. 355–362. The present Chapter is this paper with illustrations and additional remarks.

[2] E. Thompson Seton, *Life-histories of Northern Animals, An Account of the Mammals of Manitoba*, New York, 1909, p. 309.

[3] *Ibid.*, pp. 328–329.

of from 6 to about 12 feet above the ground. Two of these fruit-bodies I identified as *Armillaria mellea* and one as *Hygrophorus chrysodon*. I suspected that the destructive agent had been a Red Squirrel, for Red Squirrels were not uncommon in the woods. On October 6 my suspicions were confirmed. On that day I was approaching the Lake of the Woods and, just as I came to its

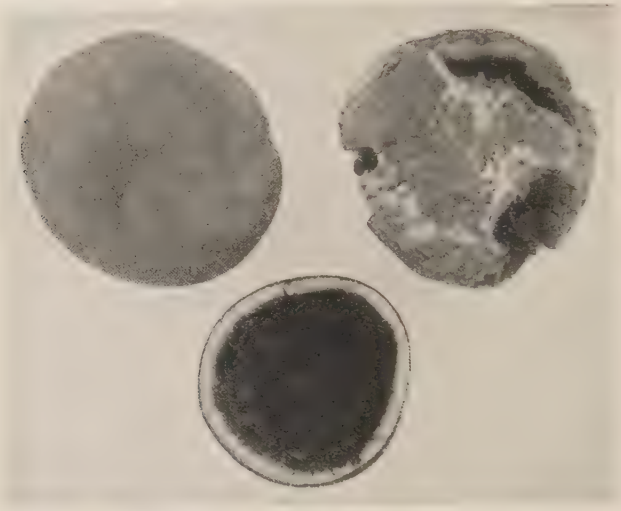


FIG. 70.—*Elaphomyces granulatus*, a fungus with subterranean fruit-bodies. The right-hand fruit-body, which has been partially devoured, was found upon the surface of the ground in Oxshott Woods, Surrey, England. As shown by the tooth marks it was unearthed by a rodent, in all probability by a squirrel. Found and photographed by Somerville Hastings. Natural size.

margin, I saw a Red Squirrel on the top of a wood-pile close by the water's edge not 20 feet away. I stood still and observed that the squirrel was sitting on its hind legs with its tail curled over its back and was engaged in eating an agaric held in its fore-paws. I watched this little scene for some moments and then drew nearer, whereupon the squirrel suddenly dropped the fungus and darted away. I then went up to the wood-pile and recovered the fungus, which proved to be a fruit-body of *Armillaria mellea*. The pileus had been eaten all around the periphery ; but the disc showed the characteristic honey colour and scales, and the stipe still retained its annulus and its peculiar dingy yellow base. On the ground at the

foot of the wood-pile I found a clump of *Armillaria mellea* fruit-bodies, some of which had been broken off by a rodent. Doubtless,

FIG. 71.—*Sciurus hudsonicus*, the Red Squirrel of North America. From Ernest Thompson Seton's *Life Histories of Northern Animals* (copyright, 1909). By courtesy of E. T. Seton and Charles Scribner's Sons. About $\frac{3}{5}$ life size.

this clump had been the source of the fruit-body which the squirrel had been eating.

On October 10, 1920, at Kenora, I observed a Red Squirrel in a Spruce-tree (*Picea canadensis*) eating the fruit-body of an agaric. The squirrel was about 12 feet above my head. After watching it for a short time, I frightened it, whereupon it deliberately placed

the fungus in a fork of the tree made by two twigs and then dashed away.

On November 3, 1920, at Kildonan Park, Winnipeg, I saw a Red Squirrel about 10 feet up a tree with a fungus in its paws. As I approached, the squirrel dropped the fungus. I picked it up and found that it was a much damaged fruit-body of *Pleurotus ulmarius*. A few minutes later I observed another Red Squirrel on a branch eating an agaric which, from where I stood, looked like *Pleurotus ulmarius*; but, when I frightened the squirrel, it carried the fungus to the top of a tall Cotton-wood Poplar and so I was unable to procure it for exact identification.

FIG. 72.—*Sciurus hudsonicus*, the Red Squirrel of North America, in characteristic attitudes. From Ernest Thompson Seton's *Life Histories of Northern Animals* (copyright, 1909). By courtesy of E. T. Seton and Charles Scribner's Sons.

Dr. W. P. Fraser, Plant Pathologist of the Dominion Division of Botany, made the following statements to me: "In some of the woods in Pictou County, Nova Scotia, Red Squirrels are very numerous. Many scores of times I have seen these animals carrying or eating the sporophores of Hymenomycetes. A squirrel, after seizing a sporophore upon the ground and before eating it, usually carried it to the top of a stump or log or up to one of the branches of a tree. Partially devoured sporophores were often left lying about on stumps, logs, etc. Most of the fungi were Russulae."

Dr. E. M. Gilbert of the Botanical Department of the University of Wisconsin told me that in the woods of Wisconsin he had often watched squirrels picking fungi, running with them along the

ground, carrying them up trees, and eating them on the branches. When making these observations, he usually lay on the ground with his head resting on a cushion. Among the fungi carried up into the trees were various species of Russula and also a Cantharellus parasitised by *Hypomyces transformans* Pk. Recently he wrote to me as follows :

" During the years 1910–1915 I spent some weeks each summer at a cabin in Douglas County, Wisconsin, and observed from time to time that some animal had been feeding upon various mushrooms common in the woods in the vicinity of the cabin. This did not cause me any concern until the summers of 1914 and 1915, when I was interested in collecting some of these fungi for cytological study. As many of the fungi I had planned to use had become mutilated, I decided to find the culprit ; so I went into the woods, stationed myself where I should not be conspicuous, and watched. Soon I found that the Red Squirrels were actively feeding on a number of Basidiomycetes, among which were :

Psalliota campestris, Hydnum repandum,
Polyporus betulinus, Hydnum caput-ursi ;
Clavaria pyxidata,

but they seemed to prefer, above all other fungi, a Cantharellus which was parasitised by a Hypomyces. At one time I found a squirrel nibbling at the fresher growth of a *Fomes fomentarius*. During the past summer, 1920, I observed that the Red Squirrels here at Madison were often feeding on the Russulae ; and frequently I have found various Morchellae partly eaten, but have never caught the squirrel in the act."

The following observations were made by Mr. E. E. Hubert, a forest pathologist, in the woods about Garrett Bay, Wisconsin, during September 16–20, 1921.[1]

Nuts and berries in the Garrett Bay region in the autumn of 1921 were scarce, but the fungi abundant. In many places in the woods squirrels had made a meal of a terrestrial fruit-body leaving only a part of the stem projecting upwards from the ground and bits of the cap scattered around it. A number of toadstools had

[1] I am indebted to Mr. Hubert for transmitting to me the notes of his observations.

been placed by squirrels upside down on high stumps, dead brush, and dead branches of felled trees; whilst others had been cleverly and accurately set in the crotches of branches several feet from the ground. Of certain species only the older and more mature fruit-bodies were eaten or harvested, while the younger and less mature ones were left untouched. It was particularly noticed that *Amanita muscaria*—the poisonous Fly Agaric—was never eaten or stored. Among the species gathered and stored by the squirrels were the following:

Russula rubra	Clitocybe maxima
Other Russulae	C. monadelpha
Lactarii	Tricholoma personatum (?)
Cantharellus cibarius	Boletus sp. (probably scaber)
Lentinus lepideus	

It thus appears that the Red Squirrel is just as keen a mycophagist in the State of Wisconsin as in Nova Scotia more than a thousand miles distant.

Professor J. E. Howitt of the Ontario Agricultural College told me that at Muskoka, Ontario, in the month of September, he had often seen squirrels carrying fungi about trees, and that once he had seen an Amanita so carried. Sometimes the squirrels fetched and carried fungi with great persistency for several days in succession. Doubtless they were laying up provender for the winter.

J. S. Boyce,[1] in treating of *Polyporus amarus* as the cause of dry rot in *Libocedrus decurrens*, the Incense Cedar, states that the soft fleshy or cheesy sporophores of this fungus, issuing through knots, are usually soon eaten by squirrels and microlepidopterous insects.

Perley Spaulding,[2] in giving an account of some investigations made upon the White-Pine Blister-Rust disease in the United States of America (*Cronartium ribicola* on *Pinus strobus*), makes the following remarks: "In a number of outbreak areas where

[1] J. S. Boyce, "The Dry-Rot of Incense Cedar," *Bull. No.* 871, *Bureau of Plant Industry, U.S. Dept. of Agri.*, 1920, p. 10.

[2] Perley Spaulding, "Investigations of the White-Pine Blister Rust," *Bull. No.* 957, *Bureau of Plant Industry, U.S. Dept. of Agri.*, 1922, pp. 35-36, Plate III.

pine infections were just about to produce pycnia for the first time, it was noted by several observers that squirrels ate the swollen bark from the infected parts of the branch." One of his photographs shows the blister-bearing (aecidial) central area of a disease spot in place at the base of a whorl of branches on a

FIG. 73.—*Armillaria mellea*, the Honey Fungus, a species readily eaten by the Red Squirrel of North America. The upper pileus has formed a white spore-deposit upon the lower one. Photographed at Scarborough, England, by A. E. Peck. Natural size.

tree-trunk, with the outer surrounding pycnidial zone eaten away by squirrels; and a second photograph of a tree-trunk shows that squirrels had eaten away those parts of the bark where pycnidia were forming presumably for the first time. Spaulding states that the squirrels run over the fruiting cankers and pick up aecidiospores on their fur and feet, so that to some extent they doubtless act as local carriers for the Rust fungus, thus helping to spread the Blister Rust disease.

Winter Stores of Fungi.—The Red Squirrel stores up fruit-bodies of fungi for the winter often in large quantities. The fruit-bodies are sometimes (1) stored in bulk in a hole in a tree, in an old crow's nest, or in some disused building, etc.; but sometimes they are (2) hung up separately in the horizontal forks of trees. When thus hung up in the autumn, they soon dry and thus become preserved until the snow is on the ground and they are required for food.

Storage in Bulk.—Mr. Stuart Criddle of Treesbank, Manitoba, in a letter to the author, says: "I have often found fungi stored by squirrels above ground but never under ground. The chief places where I have found fungus stores have been woodpeckers' holes, hollow trees, and birds' nests—especially crows' nests." Soon after writing thus, Mr. Criddle very kindly sent me a collection of dried fungi which had been stored by a squirrel in an old box in the loft of a disused house. In the collection there were 116 fruit-bodies altogether, many still quite intact, but some partially devoured and some represented only by large fragments. Of these 116 fruit-bodies, 22 were Boleti and 94 Agaricaceae. The former weighed $6\frac{1}{4}$ oz. and the latter 14 oz., so that the total weight was 1 lb. $4\frac{1}{4}$ oz. The fruit-bodies were sent to me in February and, owing to this being a very dry time of the year, they were exceedingly dry and very tough or brittle. When being gathered by the squirrel, they must have weighed many pounds. Some of the pilei bore the characteristic marks of a squirrel's incisor teeth. Many of the Boleti, and perhaps all, belonged to *Boletus scaber* (Fig. 74) or *B. versipellis* and, among the Agaricaceae, there were at least two species of Russula, at least one species of Cortinarius, a Hypholoma—possibly *H. fasciculare*, and *Lactarius piperatus*. Some of the fruit-bodies of the last-named species had been parasitised by *Hypomyces lactifluorum* and therefore showed only slight ridges beneath their pilei in place of gills.[1] A second collection of fungi sent me by Mr. Stuart Criddle from another squirrel's home at Treesbank was even larger than the first, for it contained between two and three hundred fruit-bodies.

[1] *Cf.* Chap. III, section: "The Suppression of the Gills of *Lactarius piperatus*, etc."

These, except in their larger number, resembled the fruit-bodies

FIG. 74.—*Boletus scaber*, a fleshy agaric with white pores and a roughened stipe, often consumed as food by the Red Squirrel of North America. Photographed at Scarborough, England, by A. E. Peck.

of the first collection, so that a further description of them is unnecessary.

Mr. Norman Criddle of the Dominion Department of Agriculture has informed me by letter that he has never yet found fungi mixed with the usual winter stores of squirrels but that, nevertheless, he has found " old holes in trees literally crowded with semi-dry fungi which had apparently been stored as they were gathered and not previously dried." He further states that the fungus stores were invariably abandoned so that he could never trace the owner. These stores resembled those already described and may well have been collected by the Red Squirrel.

Dr. C. N. Bell of Winnipeg has a summer house at Minaki, a village situated where the Canadian National Railway crosses the Winnipeg River, 114 miles east of Winnipeg. This house, after having been closed for the winter in the autumn of 1916, was invaded by squirrels. The squirrels stored cones and fungi in the attic and made two nests in the mattresses on the beds. The number of stored-up fungi was large. Dr. Bell wrote to me concerning the invasion of his house as follows :

" On opening my summer house on the shore of Sandy Lake in the village of Minaki in the spring of 1917, I found unmistakable evidence that one or more of the Common Red Squirrels, which play about the rocks and trees of the locality, had obtained access to the house, for there were two squirrels' nests in the mattresses on the beds and, in the attic, many gnawed pine-cones and a large quantity, say two or three quarts, of dried fungi. Also, many dried stalks of fungi were scattered about the other parts of the house accessible from the attic. Some individual squirrels have become so tame that they run up the steps to the veranda floor and, holding on to the wire screening, peer in on us while we sit at meals ; and, occasionally, they have eaten crumbs out of my little daughter's hand. At times they are rather a nuisance as they frequently jump from the trees to the roof of the house and scamper about in the very early morning, at the same time making their chattering noise. Closing up every crevice in the roof and attic has effectually prevented them from entering the house since 1917."

The above observations made by Messrs. Stuart Criddle and C. N. Bell prove conclusively that the Red Squirrel does store

fleshy fungi in bulk in the autumn for winter use. The air in Manitoba during the autumn and winter is very much drier than in England, so that the collected agarics dry without rotting or becoming unduly mouldy.

Storage in the Forked Branches of Trees.—When I first heard of squirrels storing fungi in the branches of trees, the story sounded in my ears like a romance and I was somewhat sceptical. However, as a result of a series of enquiries, although I myself have not as yet seen a tree with more than two fungi hanging in it, I cannot now doubt that trees laden with fungi by squirrels have been observed by others. Thompson Seton writes of them quite familiarly and his observations are supported by other observations made by M. W. Gorman in Alaska and by my personal friends and acquaintances at Winnipeg.

Thompson Seton in his well-known book on Northern Animals writes of the Red Squirrel as follows [1]:

"The second food supply in winter is mushrooms, chiefly of the genus Russula. If these were to be stored in the same way as the other provisions they would doubtless rot before they could be of service. The Squirrel stores them in the only available way, that is, in the forked branches of the trees. Here they are safe from the snow that would bury them, from the Deer and Field-mouse that would steal them, and, instead of rotting, they dry up and remain in good order until needed.

"I have seen Red-squirrels storing up these mushrooms in the Sandhills south of Chaska Lake, Manitoba, in the Selkirk Mountains, on the Ottawa, and on the upper Yellowstone River. The Squirrel's sense of private ownership in a mushroom-stored tree is not so clear as its feeling regarding a hoard of nuts it has gathered.

"During early winter in Manitoba I have once or twice seen a Red-squirrel dig down through the snow to some mushroom, still standing where it grew, and there make a meal of it.

"While camped at Caughnawanna, on September 14, 1905, I was witness of a comic display of frugality and temper on the part of a Red-squirrel. A heavy footfall on the leaves had held me still to listen. Then appeared a Chickaree labouring hard to drag

[1] E. Thompson Seton, *loc. cit.*, pp. 326–327.

an enormous mushroom. Presently it caught in a branch, and the savage jerk he gave to free it resulted in the 'handle' coming off. The Squirrel chattered and scolded, then seized the disc, but again had the misfortune to break it, and now exploded in wrathful splutterings. Eventually, however, he went off with the largest piece and came back for the fragments one by one.

"The scene was an exact reproduction of one described by Dr. Merriam in 1884."

Thompson Seton evidently thinks that the tree-fork mode of storage is the only kind of storage for fungi resorted to by the Red Squirrel, but in this he is in error, for, as I have shown by citing the observations of Stuart Criddle and C. N. Bell, the Red Squirrel often stores up fungi in bulk in various holes and cavities. I suspect, but am not sure, that bulk-storage in holes and cavities is more common than storage in the branches of trees.

M. W. Gorman, who has botanised in Alaska, is reported by W. A. Murrill as having made the following statement [1]:

"In the region west of the Yukon River the small red or 'pine' squirrel lives during the winter upon the seeds of *Picea alba* and mushrooms. The latter are collected in large quantities during the summer and placed in the forks of branches and other secure spots above the ground to dry." Three different kinds of brownish-coloured agarics were noticed by Gorman, who says that the squirrels visit their collections every day, even in the coldest weather.

The two following statements sent to me in writing by Mr. Ernest Hiebert and Mrs. Doern, both of whom are known to me as careful observers, supplement one another and prove in the clearest manner that, in Manitoba, the Red Squirrel not only stores fungi in particular trees in the autumn, but also feeds upon the fungi so stored during the winter.

Mr. Ernest Hiebert thus recounts his observations:

"In the middle of August, 1917, at Sandy Hook, near Gimli, Manitoba, I noticed what appeared to be a mushroom stuck between the lower branches of a spruce tree. Upon closer examination I discovered several more fungi in the same tree to the number

[1] W. A. Murrill, *Animal Mycophagists*, Torreya, vol. ii, 1902, pp. 25–26.

of twelve in all. Most of them were in the lower branches about fifteen feet from the ground and a few as high as forty feet from the ground. They had all been placed between the horizontal forks of the twigs in the upright position in which they grow. I removed several of these fungi and found them quite dry and all apparently belonging to the genus Russula except one, which I took to be *Lactarius piperatus*.

"Several days later, in the same grove of spruce trees, I came across a common red squirrel carrying a fungus along the ground. Upon being pursued it dropped the fungus, which proved to be a perfectly fresh Russula."

Mrs. A. H. Doern's observations were made in a suburb of Winnipeg and are still more interesting. She says :

"In October, 1918, I noticed a common red squirrel carrying a mushroom up one of the trees which grew in my yard at Norwood. The fungus was then placed between the twigs so that the gills looked downwards. Several more mushrooms were placed in a similar position in the same tree ; and, during the winter that followed, I repeatedly watched the squirrel eat of these dried mushrooms. The squirrel would remove a mushroom from the twigs on which it had rested, nibble at it, and then replace it as before but in some other part of the tree. Finally, during a cold spell in mid-winter, the mushrooms which still remained all disappeared from the tree and, after this, the squirrel failed to return."

Another observer who has watched squirrels taking fungi up into trees and storing them there is my friend and colleague, Dr. Gordon Bell, who writes as follows :

"I have often seen squirrels carrying pieces of fungi up into trees. At Fox Lake in Ontario there was a large pinkish fungus which was very common in the woods and which interested me because I wished to find out whether or not it was edible. One day in the latter part of August, for fully fifteen minutes, I watched a red squirrel carry pieces of the fungus up into a pitch-pine tree and deposit them in the forks made by the branches. I have also seen squirrels in Fort Rouge, Winnipeg, carrying pieces of a Peziza-like fungus up into trees. I think it highly probable that

the squirrels eat these fungi after they have dried, but I cannot assert this from actual observation."

From the foregoing evidence, it appears that the storing of fungi in the branches of trees in the autumn by the Red Squirrel is a well-developed instinct. It is remarkable with what care the fungi are deposited. The fork of a branch is first selected and then the stipe is pushed downwards through it so that the pileus rests on the twigs, the result being that the fruit-body as a whole cannot fall to the ground by its own weight or be easily dislodged by the wind or by the swaying of the branches. The trees chosen by the squirrels for their open larders are usually Spruce-trees.

The Storage of Fungi in Relation to Climate.—In England, during the late autumn and winter, as is well known, the climate is mild, the rainfall heavy, and the periods of frost not very intense or long continued. The English squirrel lays up for the winter a store of nuts and seeds but, so far as is known, never any fungi. Fleshy fungi, if stored by this animal either in holes or on the branches of trees, would, owing to the dampness and mildness of the English climate, surely be apt to go rotten rather rapidly. On the other hand, in the inland parts of Canada and of the northern United States, the climate, during the late autumn and winter, is relatively very cold, the precipitation relatively slight and in the form of snow, and the frost very severe and prolonged. In central and western Canada and in North Dakota, snow lies upon the ground and the earth is frost-bound for at least four months each year. In the northern part of North America, therefore, the storage of winter food supplies by squirrels is even more important than in England. The Red Squirrel lays up for the winter not merely cones and nuts but, in addition, a store of fungi. Owing to the dryness and coldness of the climate, the fungi hung in the branches of trees by squirrels in late autumn dry without rotting and remain good to eat until the spring comes, while those deposited in bulk in holes, although moist when collected, become partially dried and, in this condition, preserved by the action of the frost. The fungi heaped together in holes, etc., are put by the weather into a state of cold storage resembling that in which mankind now preserves many of his food-stuffs,

such as beef and mutton. The storage of fungi for the winter, by increasing and varying the supply of food, is undoubtedly beneficial to the Red Squirrel and is due to an instinct which appears to have been developed in response to severe winter conditions.

Two Chickens Hung in a Tree.—Mr. J. B. Wallis, Principal of the Machray School, Winnipeg, once observed a squirrel which, instead of storing fungi in the branches of a tree, hung up there two chickens. As is well known, the Red Squirrel robs birds' nests and kills birds freely. The killing of the two chickens, therefore, was not very extraordinary; but the hanging of the chickens in the forked branches of a tree was a very curious and unusual proceeding, and suggests that for once the fungus-storing instinct had become perverted. Mr. Wallis has written to me concerning the incident as follows:

"A red squirrel had taken up its abode just behind a farm-house near Thornhill, a village some eighty miles W.S.W. of Winnipeg. This squirrel had become quite friendly and showed no fear of its human neighbours. One day, whilst visiting the house, I was called outside and here was the squirrel laboriously dragging by the neck, up a small oak-tree, a chicken nearly as big as itself. On looking more closely, two other chickens were discovered, hung by their heads in forked branches. The three chickens had all been killed by bites at the back of the head. The squirrel, on perceiving my friend and myself, immediately seemed to sense disapproval of his thrifty habits and retired rapidly to a high bough from whence he was dislodged with a charge of number six shot. As a really advanced squirrel, he thus fell a victim to his very advancement."

Summary.—The Red Squirrel of North America not only feeds on the seeds of fir-cones, hazel-nuts, etc., but is also an habitual mycophagist. In the late autumn, it often collects fleshy fungi in large numbers for its winter supply of food, and it stores these fungi sometimes *en masse* in holes in tree-trunks, old birds' nests, etc., and sometimes on the branches of certain trees.

CHAPTER VIII

SLUGS AS MYCOPHAGISTS

Introduction—Slug-damaged Fungi in an English Wood—Slugs and Poisonous, Acrid, or Cystidia-bearing Agaricineae—Absence of Slugs from a Wood in Central Canada—Some Conclusions—The Finding of Fungi by Slugs—Previous Chemotactic Experiments—New Chemotactic Experiments—Experiments I. II, III, IV, V, VI, and VII—Slugs and Mustard Gas—Conclusions

Introduction.—Slugs eat many fleshy fungi; and in woods and gardens in Western Europe one can often find fruit-bodies which have been more or less damaged by these animals. Fungi, therefore, especially in certain localities and in certain seasons, must be considered as an important source of slug food. Among the fungi which slugs attack may be mentioned: species of Amanita, Pleurotus, Russula, Psalliota, Coprinus, Boletus, Polyporus, and Phallus. Leathery fungi, *e.g. Polystictus versicolor*, *Stereum hirsutum*, and *Schizophyllum commune*, and gelatinous fungi, *e.g. Hirneola auricula-judae* and *Auricularia mesenterica*, are generally avoided. A few experiments upon the edibility of fungi for slugs are recorded in Volume I of these *Researches*.[1]

A fruit-body which has been partially eaten by a slug can be easily recognised: (1) by the peculiar manner in which it has been rasped and mined, and (2) by the slug's slime tracks. Slugs are nocturnal animals. During the day, they hide under soil or in dark crevices; but, as darkness comes on, they emerge from their places of concealment and seek their food. They therefore visit the fruit-bodies of fungi during the night, but, as a rule, retire from them with the advent of day. Sometimes, however, a slug which has made a hole on the under side of the pileus or in the top

[1] Vol. i, 1909, p. 229. In *Trans. Brit. Myc. Soc.*, vol. vii, 1922, pp. 270–283, I published a paper called "Slugs as Mycophagists." The present Chapter is that paper with illustrations and additional remarks.

of the upper part of the stipe of a large agaric, such as *Boletus luteus* or *Lactarius piperatus*, remains half-hidden in the hole throughout the day and then may be found by the observer.

Fig. 75 shows the upper surface of a pileus of *Russula heterophylla* which had been mined under natural conditions in a wood

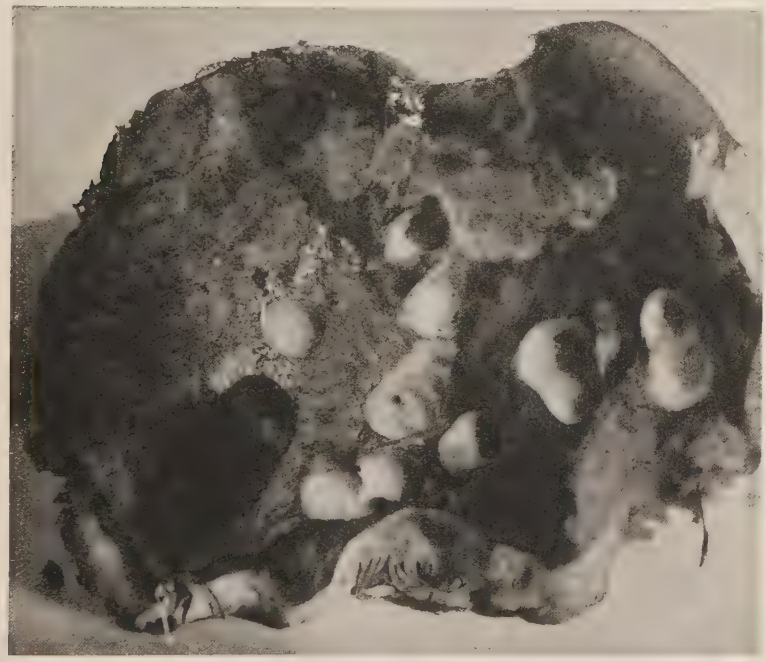


Fig. 75.—The upper surface of the green pileus of a fruit-body of *Russula heterophylla* in which large more or less hemispherical holes have been made in the white pileus-flesh by the slug, *Arion subfuscus* var. *aurantiaca*, when feeding. The slug is resting in the humped-up position, and from its body to the middle of the upper edge of the pileus extends a slime track. From a wood at Earlswood, near Birmingham, England, Sept. 8. Natural size.

by *Arion subfuscus* var. *aurantiaca*. The slug which did the damage is to be seen resting on the pileus humped-up like a disturbed *Arion ater*. Fig. 76 shows the damage done by another *Arion subfuscus* to the hymenial tube-layer of a *Boletus elegans*.

Slug-damaged Fungi in an English Wood.—On September 8, 1920, accompanied by Mr. W. B. Grove, I spent an afternoon in a wood at Earlswood, near Birmingham, England, investigating the damage which the slugs had done to the fungi. Out of several

hundreds of fruit-bodies of fleshy Hymenomycetes observed, I found very few which had not been visited and partially eaten by slugs. Some of the fruit-bodies had been absolutely ruined by these animals. Thus the stipe of a large *Boletus flavus* had been eaten in two; and the separated pileus had completely lost all its hymenial tubes, whilst the pileus-flesh had become reduced to a thin perforated shell. A slug was found ensconced in one of the cavities of the flesh; and, doubtless, it was only waiting for the night to sate its voracious appetite once more upon the wreck to which it was clinging. Some other fruit-bodies, *e.g. Russula ochroleuca*, *Lactarius piperatus*, and *L. turpis*, were almost equally damaged. The following species were found to have been visited and partially eaten by slugs:

Species Attacked by Slugs.

Amanita rubescens	Laccaria laccata
Amanitopsis vaginata	Hypholoma fasciculare
Clitocybe clavipes	H. sublateritium
Russula emetica	Flammula sapinea
R. ochroleuca	Paxillus involutus
R. sardonia	Cortinarius anomalus
R. heterophylla	C. paleaceus
R. nigricans	C. caninus
R. adusta	C. rigidus
Lactarius piperatus	Boletus flavus
L. subdulcis	B. chrysenteron
L. glyciosmus	B. scaber
L. turpis	Clavaria cinerea

The following species were found not to have been eaten by slugs:

Species Not Attacked by Slugs.

Lactarius quietus	Inocybe geophylla
L. rufus	Tubaria furfuracea
Collybia butyracea	Cortinarius sanguineus
Flammula inopus	Polystictus versicolor
Inocybe asterospora	Lycoperdon pyriforme

Of the species attacked, some, *e.g.* the Russulae, were damaged much more than others. Scarcely a single fruit-body of any species of Russula could be found which had not been partially eaten. Very

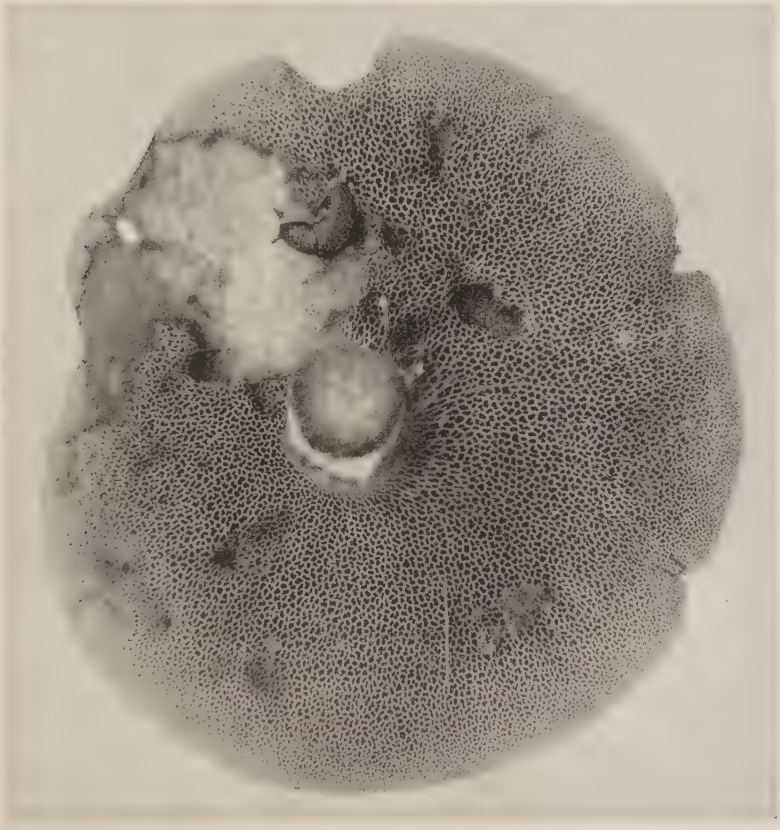


Fig. 76.—Under surface of a pileus of *Boletus elegans* showing the ravages made in the hymenial tube-layer by a slug. The slug, *Arion subfuscus*, has one of its long horns partially extended. Photographed in Ockeridge Woods, near Worcester, Sept. 21, by Somerville Hastings and the author. Natural size.

few of the fruit-bodies of *Hypholoma fasciculare*, *Laccaria laccata*, and *Lactarius glyciosmus* had been eaten and these only slightly, so that it seems that slugs do not much relish these species.

Of the species not attacked by slugs only single fruit-bodies were found of *Flammula inopus*, *Inocybe asterospora*, and *Cortinarius sanguineus*, and a few fruit-bodies only of the relatively tiny

Inocybe geophylla and *Tubaria furfuracea*, so that it is possible that, if the fruit-bodies of these fungi had been more numerous, some of them might have been found attacked. The species which seemed to have been definitely avoided by slugs were *Lactarius quietus*, *L. rufus*, *Collybia butyracea*, *Polystictus versicolor* and *Lycoperdon pyriforme*.[1]

Two species of slugs were found upon the fungi, a larger reddish one about one inch long (Fig. 75) and a smaller darker one. Mr. P. T. Deakin kindly identified the former as *Arion subfuscus* var. *aurantiaca* and the latter as a Limax. The specimens submitted for the Limax were too immature for exact identification.

Polystictus versicolor, *Stereum hirsutum*, and other tough and leathery fungi, are probably protected against the ravages of slugs by their physical consistence; while *Lactarius quietus*, *L. rufus*, *L. glyciosmus*, *Collybia butyracea*, *Laccaria laccata*, and *Lycoperdon pyriforme* are more or less protected against slugs by their chemical contents. The majority of fleshy fungi, however, seem to be in no way protected against slugs, and some of the commonest species, *e.g.* those of Russula, Amanita, Amanitopsis, and Boletus, often suffer most. On the whole, the most soft-fleshed species seem to be the most relished by slugs, and these animals are particularly fond of the soft parenchymatous tissues of the Russulae and of the soft hymenial tubes and flesh of many Boleti. Voglino has supposed that slugs are important agents in bringing about the dissemination and germination of the spores of Russulae, etc., and is inclined to believe in the existence of symbiotic relations between slugs and Hymenomycetes.[2] I am rather of the opinion that, when a slug attacks a fruit-body, the advantage is chiefly, if not entirely, on the side of the slug and that, from the point of view of the fungus, the slug is a troublesome ectoparasite. As I pointed out in Volume I, the fruit-bodies of the Hymenomycetes are beautifully organised to secure the dissemination of the spores by the wind and their injury by slugs certainly prevents a great many spores from being liberated.[3]

[1] These five species are also distasteful to human beings.
[2] *Vide* these *Researches*, vol. i, 1909, pp. 226–227.
[3] *Ibid.*, p. 228.

Benecke [1] has recently made some experiments on slugs by offering them definite chemical substances; and he has thereby found: that *Arion empiricorum* and *A. subfuscus* readily consume agar preparations, etc., containing sugar or proteins; that *Agriolimax agrestis* prefers sugar; and that *Limax tenellus* avoids sugar in higher concentrations. Cubes of agar containing only water or other indifferent substances were refused. Certain stimulatory substances, as Stahl found, appear to be required to make the food palatable. As such stimulatory substances Benecke mentions: sugar, peptone, and glycogen for *Arion empiricorum* and *A. subfuscus*; sugar for *Agriolimax agrestis*; and glycogen for *Limax tenellus*.

Fig. 77.—*Amanita phalloides*, the Death Cap, an agaric which, although very poisonous to man, is eaten with impunity by slugs. The pileus shows damage done by slugs under natural conditions. About the natural size. Photographed at Scarborough, England, by A. E. Peck.

Slugs and Poisonous, Acrid, or Cystidia-bearing Agaricineae.—Certain fungi which are very poisonous to man are eaten with impunity by slugs. Thus in August, 1922, at Earlswood, I observed both *Arion subfuscus* and *A. ater* feeding on *Amanita pantherina*; and, as is well known, one not infrequently finds in English woods slug-damaged fruit-bodies of the Death Cap, *Amanita phalloides* (Fig. 77), the Fly Agaric, *A. muscaria* (Fig. 78), *Boletus luridus*, and other poisonous species. According to Benecke [2] *Amanita phalloides*, excepting the pellicle and the volva, is eaten with avidity by *Arion empiricorum* and *A. subfuscus* but is refused by *Limax tenellus* which lives largely on fungi and by *L. arborum* which is supposed to live only on lichens. Experiments, recorded in Volume I, showed that *Limax maximus*, *Arion subfuscus*, and *Agriolimax agrestis* all eat freely of *Amanita muscaria* without

[1] W. Benecke, "Pflanzen und Nachtschnecken," *Flora*, Bd. CXI and CXII (Stahl Festschrift), 1918, p. 475.

[2] W. Benecke, *loc. cit.*, pp. 470–471.

suffering any harm.[1] In this respect these molluscs resemble the larvae of the fungus gnats (Mycetophilidae) which are often to be seen in large numbers mining their way through the flesh of the pileus, but differ from house-flies, which quickly become stupefied when they sip the hyphal sap, and from cats, dogs, man, and other carnivorous mammals, to which the fungus may even prove fatal. Why the toxic substances present in the Amanitae should be deadly to some animals, such as house-flies and man, and harmless to others, such as slugs and the larvae of certain fungus gnats, has never yet been sufficiently explained; but for a solution of the problem we must look to the biochemist.

It is possible that slugs and fungus gnats have been dependent on fleshy fungi for food for a period of geological time amounting to some tens of millions of years.[2] The immunity of these animals to fungus toxins may therefore have been brought about by natural selection, those individuals which suffered least from eating poisonous fungi having survived and left descendants. On the other hand, the house-fly, the cat, man, etc., which have come into contact with fungi either not at all or only occasionally, have never had a chance to become immune to the poisonous species.

I have collected evidence which goes to prove that cows may eat a considerable number of *Amanita muscaria* fruit-bodies without suffering in any marked degree. It therefore seems probable that herbivorous mammals, which, like slugs, in the course of evolution have fed in an environment where poisonous fungi have been available as food, are far less susceptible to fungus poisons than carnivorous mammals which do not eat vegetables and therefore never come into contact with fungi. Cows, like slugs, may have acquired their relative immunity to the toxins of the Amanitae, etc., through the process of natural selection.

Russula emetica, the juice of which is acrid to man, is evidently regarded as a tit-bit by slugs, for in English woods one often finds its pilei partially or completely destroyed by these animals. In 1909, I showed that, under experimental conditions, *Limax maximus*, *Arion subfuscus*, and *Agriolimax agrestis* all eat *Russula*

[1] A. H. R. Buller, these *Researches*, vol. i, 1909, p. 229.
[2] *Re* fossil Mycetophilidae, *ibid.*, pp. 19–20.

emetica with avidity.[1] Dr. W. T. Elliott[2] has recently confirmed and extended this observation, for in his experiments he has found that *Russula emetica* is either completely devoured or eaten with avidity by the following seven slug species: *Arion ater*, *A. subfuscus*, *A. intermedius*, *A. hortensis*, *Limax maximus*, *L. cinereo-niger*, and *Agriolimax agrestis*. However, Benecke[3] has observed that in captivity, in long-continued experiments, such slugs as *Limax cinereo-niger* and *L. empiricorum* prefer the milder Russulae, *e.g. R. cyanoxantha*, *citrina*, *alutacea*, *lutea* and *integra*, to the sharper ones, *e.g. R. emetica*, *fragilis*, *sardonia* and *pectinata*.

Pluteus cervinus, *Inocybe rimosa*, *Coprinus micaceus*, etc., contain numerous cystidia, those of *P. cervinus* being provided with recurved terminal hooks. Yet they are all ravaged by certain slugs.[4] It thus appears that the cystidia are non-protective so far as slugs are concerned.

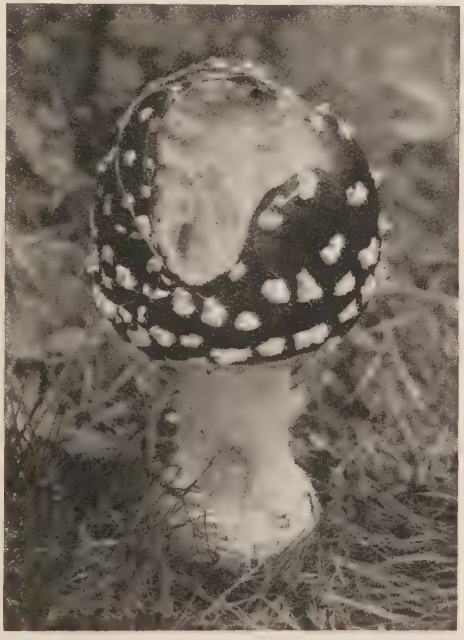


FIG. 78.—*Amanita muscaria*, an agaric which, although poisonous to man, is eaten with impunity by slugs. A slug has made a large hole in the pileus and a smaller one in the stipe. Photographed in Wyre Forest, Worcestershire, by Somerville Hastings. $\frac{2}{3}$ natural size.

The fact that fleshy fungi in general are unprotected against the

[1] *Researches on Fungi*, vol. i, 1909, p. 229.

[2] W. T. Elliott, *in litt.* His paper entitled "Some Observations on the Mycophagous Propensities of Slugs" is shortly to appear in the *Trans. Brit. Myc. Soc.* In this paper Dr. Elliott states that on two occasions *Arion ater* died after eating *Russula emetica* with avidity. To settle whether or not the slug was poisoned by the fungus, it seems to me that further experiment is required.

[3] W. Benecke, *loc. cit.*, pp. 465–466.

[4] Observations made by myself and by W. T. Elliott (*in litt.*).

attacks of slugs finds its analogy in the fact that meadow grasses in general are unprotected against the attacks of horses and cattle. In both instances the individual plants are so numerous that the partial destruction of some, or even many, of them has not been a cause sufficient in the course of evolution to bring about the development of protection by mechanical or other means. A change in the consistence of our terrestrial agarics from soft-fleshy to a degree of mechanical hardness or toughness which would be protective against slugs would, of necessity, be accompanied by a larger expenditure of fungus material and energy, by a slower rate of development, and by a smaller output of spores per unit mass of mycelium. Thus the protection of fleshy fungi by mechanical means might be purchased at too great a price.

Absence of Slugs from a Wood in Central Canada.—Slugs, which are common in England and in the extreme west of Canada (British Columbia), where the climate is damp and moderately warm, are rare in central Canada, where the climate is very dry and relatively cold. Most native-born Manitobans, so far as I can find out by enquiry, have never seen a living slug; and there can be no doubt that the big species of Limax, Arion, etc., which abound in gardens and woods in England, are entirely absent from central Canada.

In the late autumn of 1920, I spent several days at Kenora on the Lake of the Woods, central Canada, studying the fleshy fungi in the woods; and, although I made a careful search, I could not find a single agaric damaged by a slug.

In the autumn of 1921, I was again at Kenora, and again noted the freedom of the fleshy agarics from slug damage. However, on this occasion, under a rotten log in a wood not far from dwellings, to my surprise, I came upon two small slugs. These were dark brown or blackish and about half an inch long, and they had evidently been feeding upon the delicate pilei of some *Trogia crispa* fruit-bodies which were attached to the log in their immediate vicinity. They appeared to belong to the genus Agriolimax and may have been *A. campestris*.

According to Frank C. Baker,[1] *Agriolimax campestris* and

[1] *In litt.*

A. hyperboreus have both been reported from Manitoba, and the only other species likely to be found in such a cold northern region is *Philomycus carolinensis*.[1]

Since fleshy fungi, *e.g.* Russulae, Lactarii, Amanitae, Cortinarii, etc., occur in great variety and numbers in the woods of central Canada, and since slugs do not occur in these woods or are very rare there, it seems safe to infer that fleshy fungi, such as Russulae, Lactarii, Amanitae, Cortinarii, etc., in no way depend upon slugs for the dissemination or germination of their spores.

Some Conclusions.—We may conclude from the above observations: (1) that slugs, under natural conditions, may attack and feed upon most species of fleshy Hymenomycetes occurring in woods; (2) that the attacks of the slugs often seriously interfere with the production and liberation of spores by individual fruit-bodies; (3) that most species of fleshy fungi are in no way protected against slugs; (4) that slugs feed with impunity on fungi which are poisonous to man; and (5) that very many species of fleshy fungi do not depend upon slugs for the dissemination or germination of their spores.

The Finding of Fungi by Slugs.—Before eating a fungus, a slug must first find it. Now, according to zoologists, the common slugs of English fields and woods, *e.g. Limax maximus* and *Arion ater*, although possessing eyes, can see clearly for a distance of only 1 or 2 mm. and find their food chiefly by their sense of smell.[2] We must therefore suppose that slugs find the fungi upon which they feed chemotactically, *i.e.* by changing their direction of

[1] *Agriolimax agrestis*, the common field slug, introduced from Europe, is now widely distributed in eastern North America and has become a veritable pest in gardens in some parts of the United States (*vide* F. C. Baker, "A Mollusc Injurious to Garden Vegetables," *Science*, N.S., vol. xliii, 1916, p. 136; also "A Molluscan Garden Pest," *Science*, N.S., vol. xlvii, 1918, pp. 391–392). I myself have seen this small slug in a greenhouse at Winnipeg and have had other specimens brought to me from a Winnipeg garden; but Winnipeg gardeners in general are unacquainted with it, and, so far as I know, it has never yet been found in woods away from habitations. *A. agrestis* is very partial to chlorophyllaceous food, *e.g.* lettuce, cabbage, etc.; but, as the experiments of Dr. W. T. Elliott (communicated *in litt.*) and others have shown, it has no great liking for fungi and is only occasionally a mycophagist.

[2] V. Willem, *Arch. Biol.* XII, 1892, p. 57, cited from A. H. Cooke, *Cambridge Natural History, Molluscs*, 1895, p. 185.

locomotion in response to the chemical stimulus arising from the odoriferous substances which the fungi give off.

Previous Chemotactic Experiments.—As evidence that slugs find their food by their sense of smell A. H. Cooke cites the following observations [1] :

"M. Parenteau was one day walking along a dusty high-road, when he noticed, near the middle of the road, an empty bean-pod and two Arions eating it. Attributing the meeting of feeders and food to mere chance, he was walking on when he noticed a second bean-pod, and, about two yards away from it, a third Arion, hurrying straight towards it. When the *Arion* had yet more than a yard to traverse, M. Parenteau picked up the bean and put it in his pocket. The *Arion* stopped, raised its head, and turned in every direction, waving its tentacles, but without advancing. M. Parenteau then carried the bean to the other side of the road, and put it in a small hole behind a piece of stone. The *Arion*, after a moment's indecision, started off straight for the bean. Again the position of the precious morsel was changed, and again the *Arion* made for it, this time without being further tantalised.

"M. Moquin-Tandon noticed, one rainy day in the botanical gardens at Toulouse, two *Limax maximus* approaching a rotten apple from different directions. He changed the position of the apple several times, placing it at a sufficient distance to be sure they could not see it, but they always hit it off correctly, after raising their heads and moving their long tentacles in every direction. It then occurred to him to hold the apple in the air, some centimetres above the head of the *Limax*. They perceived where it was, raised their heads and lengthened their necks, endeavouring to find some solid body on which to climb to their food."

As confirming M. Moquin-Tandon's experiment, and as further evidence that the olfactory sense in Limaces is extremely acute, J. W. Taylor in his *Monograph* relates the following [2] :

"Mr. L. E. Adams, about ten o'clock, one dark, windy, and

[1] A. H. Cooke, *Cambridge Natural History, Molluscs*, 1895, pp. 193–194. These observations were first recorded by Moquin-Tandon in his *Mollusques de France*, vol. i, p. 130.

[2] John W. Taylor, *Monograph of the Land and Freshwater Mollusca of the British Isles* (*Testacellidae, Limacidae, Arionidae*), Leeds, 1907, p. 37.

wet evening in August, 1897, at Clifton, Derbyshire, saw a *Limax maximus* crawling directly toward a plate upon the lawn, containing the remains of the dog's dinner ; when first observed the slug was about six feet distant from the plate, but within thirty minutes had reached it ; the plate was then removed to a second position, about six feet away, but in another direction ; the slug almost immediately changed its course, and again made straight towards the plate, on again nearing it the same process was repeated with the same result, the plate being finally removed and placed in a fourth position, eight feet away, and directly to the leeward of the slug, yet in a little more than half-an-hour the slug had reached the plate."

Ernst Stahl [1] of Jena, whilst carrying out some extended investigations upon the chemical and physical means by which certain plants are protected from the attacks of slugs and snails, incidentally convinced himself by experiment that slugs find their way to their food by their sense of smell. He placed a slug (Limax) upon a moistened dinner plate and with his mouth blew gently upon it in a horizontal direction. He found that the current of air so produced had no particular effect upon the slug's movements. He then put a cup fungus, *Peziza vesiculosa*, between his mouth and the slug and continued blowing. The slug then immediately changed its behaviour. If the slug's head had been turned away from the experimenter, the slug raised it, moved its tentacles about in the air, soon turned the front part of its body around, and then steered, as the blowing continued, straight toward the fungus. That the slug sought its food by its sense of smell and not by its sense of sight, Stahl showed as follows. He blew over the Peziza as before and waited until the slug had approached to within about 1 cm. of its surface. He then took another Peziza, placed it upon the opposite side of the plate, and blew over it toward the slug. The new current of air was thus made to move in the opposite direction to the first one and to pass over the second fungus, the slug, and the first fungus successively. Stahl then observed several times that the slug, although only 1 cm. away from the first fungus

[1] Ernst Stahl, *Pflanzen und Schnecken, Eine biologische Studie über die Schutzmittel der Pflanzen gegen Schneckenfrass*. Jena, 1888. foot-note. pp. 15–16.

and many cm. away from the second, turned itself around, left the near-by first fungus, and crawled directly toward the distant second one from which the current of air was coming. It was only when the slug was almost touching the first fungus that Stahl was unsuccessful in trying to induce the slug to turn around and seek the second.

New Chemotactic Experiments.—With a view to testing the supposition that slugs find their food, and in particular find fungi, by their sense of smell, I have made a series of experiments, under conditions as natural as possible, upon the attraction of *Limax maximus* to *Phallus impudicus* and to certain Hymenomycetes. Before giving an account of these experiments, however, it will be necessary for me to make a few preliminary remarks upon both the Limax and the Phallus.

FIG. 79.—*Limax maximus*, a slug which is a mycophagist, showing appearance when crawling toward food. The tentacles are swollen terminally to form olfactory bulbs, the eyes being subterminal on the longest pair of tentacles. The fore part of the body bears the mottled mantle with its respiratory aperture. The hind part of the body is striped. About $\frac{2}{3}$ natural size. From Vol. III of the *Cambridge Natural History*, by courtesy of Macmillan & Co.

According to Simroth and Scharff, the food of *Limax maximus* (Fig. 79) consists of non-chlorophyllaceous substances, while anything containing chlorophyll is as a rule refused [1]; and W. A. Gain considers *Limax maximus* a very dainty feeder, preferring fungi to all other foods.[2] Stahl [3] divided slugs and snails into *omnivora* and *specialists* and states that *Limax maximus* is a specialist which feeds chiefly on fungi.[4]

[1] A. H. Cooke, *loc. cit.*, p. 31.

[2] *Ibid.*, p. 32.

[3] E. Stahl, *loc. cit.*, p. 15.

[4] Benecke (*loc. cit.*, p. 474, etc.) has recently divided slugs into: (1) *pleophagous* (*Arion empiricorum*) which eat a great variety of fungi, green leaves, roots, and fruits of flowering plants; (2) *herbivorous* (*Agriolimax agrestis*) which prefer green plants to fungi whenever a choice can be made; and (3) *mycophagous* (*Limax tenellus*) which eat a great variety of fungi and prefer fungi to higher plants whenever a choice can be made. Doubtless, according to this scheme of classification, *Limax maximus* would be regarded as *mycophagous*.

Limax maximus, like most other slugs, hides during the day in crevices under stones or in the soil, and only emerges from its place of retreat as darkness is coming on. It was therefore necessary for me to make my experiments during the evening and night. Slugs and snails possess to a considerable degree the power of *homing*, *i.e.* of returning to the same hiding-place day after day, after their night excursions in search of food.[1] My observations have convinced me that *Limax maximus* is a homing slug. The slugs used in my experiments had a fixed abode to which they always returned after their nocturnal peregrinations ; and the realisation of this fact was of considerable help to me in suitably arranging the position of the fungus fruit-bodies which I wished the slugs to visit.

It has been calculated that an average-sized snail of moderate pace progresses at the rate of about a mile in 16 days and 14 hours.[2] This works out at about 13·3 feet per hour. The rate of movement of *Limax maximus* is probably not very different from that of a snail. On one occasion I found that a *Limax maximus* had travelled from one point to another 12 feet distant in 1 hour and 20 minutes ; but the course taken was not the shortest possible, so that I have no doubt that the actual pace of the slug somewhat exceeded 10 feet an hour.

Phallus impudicus—the Stink-horn Fungus—as every botanist is aware, is one of the most remarkable of all fungi. The young fruit-body—sometimes known as a Devil's Egg—is a soft spherical white ball, a little larger than a hen's egg ; and it is protected upon its exterior by a thick gelatinous peridium. At maturity, the ball suddenly bursts at the top, and then there emerges from it in the course of about half an hour a sort of Jack-in-the-Box made up of a long, white, hollow, spongy, bread-like stipe bearing at its free end a conical cap covered with dark green slime (Fig. 80). The slime contains sugar and millions of green spores, and from it issues a very powerful and offensive odour. Dung flies are attracted to the fungus by the smell, alight upon the green cap, lick up the sweet slime, and carry away the spores upon their straggling legs and inquisitive proboscides and within their alimentary canals.

[1] A. H. Cooke, *loc. cit.*, pp. 34–36. [2] *Ibid.*, p. 46.

FIG. 80.—*Phallus impudicus*—a fungus which attracts both dung-flies and slugs. A fruit-body just after expansion showing: (1) the dark-green, spore-containing, sweet, malodorous, glebal fluid which covers the cap and serves to attract flies; (2) the white bread-like stipe which is sought out and eaten with avidity by the slug, *Limax maximus*; and (3) the ruptured gelatinous peridium. From Sutton Park, Warwickshire, England. Expansion took place in the laboratory. Natural size.

Thus the spores of the fungi are disseminated through the agency of insects.

The smell from the cap of an expanded *Phallus impudicus* attracts not only flies during the day but also slugs during the night. Early in the morning I have several times found an expanded fruit-body with a stipe which had been half-eaten by slugs during the previous night (*cf.* Fig. 81), the slime left upon the fungus and the nature of the damage affording a clear indication of the identity of the marauders ; and, in the twilight of the evening, I have sometimes found a slug, *Limax maximus*, actually upon a Phallus engaged in feeding.

Experiment I.—At my father's house at Birmingham, England, there is a smooth, well-compressed, gravel carriage-way which is oval in form, 40 feet wide and 60 feet long (Fig. 82). On a border, at the edge of the gravelled area, one evening in August as darkness was setting in, I found an expanded Phallus upon which a slug, *Limax maximus*, was feeding. I removed the slug and set the fungus upon the gravel at a distance of 10 feet from the edge of the border. The next morning I found that a slug had visited the fungus upon the gravel, and the slime-track revealed that the slug had come from the border where I had first found the fungus with a slug feeding upon it. The track was very direct from the border to the fungus. It therefore appeared that the Phallus had attracted the slug chemotactically for a distance of at least 10 feet (Fig. 82, no. I).

Experiment II. -Shortly after making the above experiment, on August 28, 1920, I visited Sutton Park, Warwickshire, and there procured nine large Phallus balls from under a Holly bush. The balls were full-grown, but still quite odourless ; and their stipes were beginning to elongate, for I could feel them in some of the balls pressing upwards against the top of the peridium. I took the balls home to my father's garden, planted them in damp soil in pots, and set the pots in the green-house. Two days afterwards, one of the balls opened and a tall stipe covered with a strongly odorous dark-green cap emerged. In the evening I set the expanded Phallus in the middle of the gravelled area. Next morning I found that the fungus had been visited by a slug which, as indicated by

its slime-track, had crept over the gravel for a distance of about 21 feet.

Experiment III.—The other Phallus fruit-bodies opened one by one, and with them I made several other experiments like the one just described. In one of them a slug came at night about 24 feet over the gravel to two fruit-bodies which were in one pot, ate a piece out of each of the two stipes, and then crept between the bottom of the pot and the gravel (Fig. 82, no. III). When I raised the pot in the morning, in order to take it to a place where the Blue-bottle flies could not eat up all the green slime, I found the slug beneath. The slug was kindly identified for me by Mr. P. T. Deakin as *Limax maximus* var. *obscura*.

On three other nights I placed pots with expanded Phallus fruit-bodies in the middle of the gravelled area, but no slugs visited them. This may have been due in part to the paucity of slugs in the borders and in part to the weather being rainy and windy. The successful experiments were performed on still nights. Slime tracks were only found in the morning upon the gravel when a slug had visited a Phallus during the previous night.

The above observations show that *Limax maximus*, under natural conditions, guided by its sense of smell, sometimes travels from 21 to 24 feet

FIG. 81.—*Phallus impudicus*. The fruit-body has been visited by slugs which have eaten holes in the middle and base of the stipe. Blue-bottle and other flies have completely removed the green spore-containing fluid from the gleba, so that the glebal ridges are now freely exposed to view. The veil hanging from beneath the gleba is unusually well developed. Photographed at Scarborough, England, by A. E. Peck. ½ natural size.

toward an expanded fruit-body of *Phallus impudicus* and that, upon coming in contact with the fruit-body, it feeds upon the stipe.

I employed *Phallus impudicus* for my first experiments upon the chemotaxis of slugs because of its very powerful odour and the convenience with which I could procure and handle its fruit-bodies ; but I have found that similar experiments can be performed with Boleti and Agaricineae.

Experiment IV.—On September 8, I procured three fresh fruit-bodies of *Boletus scaber* from a wood and, in the evening of September 9, placed them upon the gravelled area at a distance of 10 feet from the border. During the night a slug came from the border across the gravel to the fruit-bodies and ate three holes in the top of one of the pilei. A similar experiment made at the same time with a large fruit-body of *Russula heterophylla* was also successful.

Experiment V.—The next evening, September 10, about 8 P.M., I placed upon the gravel three little heaps of hymenomycetous fruit-bodies. In the first heap were the three fruit-bodies of *Boletus scaber* which had been used the night before, in the second three fruit-bodies of *Cortinarius caninus*, and in the third three fruit-bodies of *Russula nigricans*. Each heap was made at a distance of 12 feet from the border and the three heaps were in a row, the central heap being that of *Boletus scaber* and the intervals between the heaps being 4 feet. Having had considerable difficulty in some of the previous experiments in tracking the slime-trail upon the gravel owing to the intermittency or thinness of the trail and owing to the effects of dew, I placed some large fern leaves in a line along the edge of the gravel by the border, so that, if a slug crossed the line, it would leave a trail behind which could be easily detected. The night was a very dark one. About 10 P.M. I went out with a lighted taper to see what was happening. On examining the fern leaves I found upon the leaflets a shining slime-trail, the direction of which proved that the fern line had already been crossed by a slug. I then hunted about on the gravel and found the slug, a *Limax maximus*, about 4 inches long, actually on its way to the fungi. The slug was already 4 feet from the border whence it had come and was heading in the right direction to reach the row of

fungus heaps some 8 feet distant. I noticed, however, that the path of approach to the fungi was by no means a straight line but was made up of a series of curves. At 10.45 P.M. I found the slug

FIG. 82.—Plan of ground used for making long-distance chemotactic experiments with the slug, *Limax maximus*: *a*, the border where the slugs lived, containing ferns, blocks of sand-stone *b*, and trees *c*; *d*, a lawn; *e e*, a smooth gravel carriage-way; *f* and *i*, grass-plots; *g*, the front door step of the house *h*. The numbers I, III, VI, and VII show the positions of the fungi in Experiments I, III, VI, and VII, as described in the text. The dotted lines and arrows show somewhat diagrammatically the routes taken by the slugs for Experiments I, III, and VII. Experiments I and III were made with a fruit-body of *Phallus impudicus* contained in a pot, Experiment VI with three species of Agaricineae, and Experiment VII with two. The dimensions of the area of gravel, etc., and the distance traversed by the slugs are indicated by the scale.

about 4 feet from two of the heaps of fungi, and at 11.20 P.M. I found the slug actually upon one of the fruit-bodies of *Boletus scaber* quietly feeding. No other slug could be seen anywhere. The next morning I detected the slime-trail of the slug in the neighbourhood of the heap of Boleti but nowhere else, the trail having been weakened or destroyed by dew formation; and the

slug had disappeared. In all probability the slug had returned to the border whence it had originally come.

Experiment VI.—The next evening, September 11, I set out upon the gravel the same three heaps of fruit-bodies as had been used the night before (Fig. 82, no. VI). Again the heaps were made in a row parallel to the edge of the border, the intervals between the heaps being 4 feet, the *Boletus scaber* heap occupying the central position in the row and the *Cortinarius caninus* and *Russula nigricans* heaps the end positions. However, the arrangement of the heaps differed from that of the night before in that each heap instead of being only 12 feet from the edge of the border was now 20 feet. The condition of the *Russula nigricans* and *Cortinarius caninus* fruit-bodies was still good, but the *Boletus scaber* fruit-bodies were now in an advanced stage of putrescence. The evil state of the *Boletus scaber* fruit-bodies was perhaps the reason why, as we shall see in the sequel, they were not visited by a slug in this particular experiment. The night was again very dark and still. At 9.40 P.M., with the help of a lighted taper, I found a *Limax maximus* which had just emerged from its hiding-place and which was moving behind a block of sandstone in the border 21 feet from the fungi. At 11 P.M. I went out again and found that the slug had already travelled 11 feet upon the gravel toward the fungi from which it was now only 9 feet distant. I watched the slug for a little time but, being afraid of disturbing it too much, soon retired into the house. At 12 P.M. I sought the slug again and found it 6·5 feet away from the row of fungi; but, to my surprise, it was moving away from the row of fungi instead of toward it. At 1 A.M., the slug was 5 feet away from each of the heaps of *Boletus scaber* and of *Russula nigricans*; at 1.30 A.M., about 2 feet away; and, finally, at 2 A.M., actually upon one of the fruit-bodies of *Russula nigricans* devouring the gills. Thus the slug, after some five hours of wandering, had at last succeeded in finding one of the heaps of fungi set 20 feet from the edge of the border where the slug had first been seen.

The slug, between 9.40 P.M. and 11 P.M., must have travelled almost directly toward the fungi; for, during this period, it traversed 1 foot of border and 11 feet of gravel in the direct line of its journey. But between 11 P.M. and 1 A.M. this rapid progress

was not kept up and there was a great waste of time, for during this period the net advance of the slug toward the fungi was only 4 feet. The slug, as the track showed the next morning, seems, during these two hours, to have wandered more or less round and round in a knotted manner as if it had had some difficulty in detecting the scent of the fungi. As it happened, the slug was obliged to cross the line where the heaps of fungi had lain during the previous night and day, and it is therefore possible that the fungi had in some way scented the ground and that the scent had misled the slug. It is also possible that variations in air-currents took place in such a way as to send the odour of the fungi in the heaps toward the slug only very intermittently. But, whatever may be the true explanation, it is certain that between 11 P.M. and 1 A.M. the slug lost much time and spent a considerable amount of energy in fruitless wandering.

There was nothing upon the gravel for the slug to eat except the fungi I had placed there and, if the slug had continued in the direction in which it set out without finding the fungi, it would have traversed a gravel desert 60 feet across.

At 2 A.M., as soon as I had found the slug which had been under observation upon a *Russula nigricans* fruit-body, I hunted carefully over the gravelled area for other slugs. I could find one more slug only—another *Limax maximus*—which had come out of the border and was heading straight for the row of fruit-body heaps from which it was only 8 feet distant; but whether or not this second slug ever reached one of the heaps I cannot say, as at 2.5 A.M. I retired to bed and, in the morning, could not clearly distinguish the trail.

In the morning of September 12, I found that the slug which had visited the *Russula nigricans* fruit-bodies was no longer to be seen upon the gravel. Doubtless, it had once more retired to the border. It is probable that the return journey could not have been accomplished in less than two hours. It appears, therefore, that our *Limax maximus*, with the object of feeding upon a fungus and then returning home, must have spent some six or seven hours in a single night in wandering over the gravel where the fungus was. Such an effort shows how strongly fungi attract slugs of the *Limax*

maximus species. Doubtless, the slugs in woods are also attracted to fungi from a distance of many feet. In view of my observations on *Limax maximus*, the success with which slugs in woods find out the fleshy Hymenomycetes can no longer be a matter for astonishment.

Experiment VII.—On September 12, I made a fourth experiment with hymenomycetous fruit-bodies. On this occasion I used the *Russula nigricans* and *Cortinarius caninus* heaps alone, as the *Boletus scaber* fruit-bodies had now become thoroughly decomposed. I set the two heaps of fruit-bodies on the gravel 4 feet apart and each 21 feet distant from the place in the border from which the slugs usually issued on their nocturnal forays; but the new position of the fungi was such that the slugs, if they sought the fungi, would be obliged to travel not in the direction taken during the previous two nights but in a direction making therewith an angle of 45° (Fig. 82, no. VII). The night was very still, and dark; there was no moon, and overhanging trees shut out from that part of the gravel which the slugs would be obliged to cross even the faint light of the stars. At 11.30 P.M., with the help of a taper I found a slug moving toward the two heaps of fungi and only 9 feet distant from them. It was a *Limax maximus*, exactly resembling the two I had seen the previous night, and its four horns were spread out in the air as though they were being used to detect the direction from which the odour of the fungi was coming. I could see by the slime-trail upon fallen leaves and gravel stones that the slug was making a gentle sweep toward the *Russula nigricans* fruit-bodies and that it had kept upon a steady course since it had left the border. Next morning, I found that the *Russula nigricans* fruit-bodies had been visited by two slugs during the night, for there were four slime-tracks passing between them and the border. Moreover, one large cavity and two smaller ones had been made by the slugs in one of the pilei. By careful tracking, I found that one of the slugs which we will assume was homeward bound, after feeding upon one of the *Russula nigricans* fruit-bodies, had made a *détour* and had visited the heap of *Cortinarius caninus* fruit-bodies. Here it had crept on to one of the pilei and tasted the gills, and then it had retired by a somewhat sinuous course to the border from which it had set out, 21 feet

away. The actual distance traversed by this slug in the course of its excursion to the two heaps of fungi must have been at least 50 feet.

The circumference of a circle with a radius of 21 feet is 132 feet. The width of my heap of *Russula nigricans* fruit-bodies was 4 inches. Supposing, therefore, that the heap of fruit-bodies were on the circumference of a circle with a radius of 21 feet, as was actually the case in the experiment just recorded, and supposing, further, that a slug were to start from the centre of this circle and move at random radially outwards for a distance of 21 feet, the chances of the slug meeting the heap of fruit-bodies would be 395 to 1 against. Simple mathematical calculations of this kind afford strong evidence that the slugs in my experiments did not find the fungi in the night by chance but through the guidance of some stimulus coming from the fungi and received by their sense organs.

Immediately after making Experiment VII, I was obliged to leave England to return to duties in Canada. My investigations upon the finding of fungi by slugs were thereby brought to an end.

Slugs and Mustard Gas.—There can be but little doubt that the stimulus which comes from the fungi to the slugs and which guides these animals on their foraging expeditions is gaseous in nature. It has been recently shown by Dr. Paul Bartsch of the Smithsonian Institute, Washington, that *Limax maximus* is extraordinarily sensitive to certain gases. A few years ago a number of slugs of this species, which were under observation in his home, escaped from the box in which they had been confined. Their behaviour in the furnace room showed that they were sensitive to the fumes coming from the furnace and, in response thereto, made characteristic movements of their tentacles. After the United States entered the War and the need for a gas detector arose in connection with the fighting at the front, Dr. Bartsch recalled his furnace-room observations. A very brief period of experimentation then revealed the extraordinary sensitiveness of *Limax maximus* to mustard gas, and such startling results were obtained that within two hours after the first experiment had been made, the Allied forces were advised by cable of the possibilities of using the slug as a gas detector. Dr. Bartsch found that the tentacles of *Limax maximus* are sensitive to a dilution of 1 in 10,000,000 of mustard

gas, and that they make characteristic responses indicating the degree of dilution. Dr. Bartsch also found that man reacts to a dilution of 1 in 4,000,000. *Limax maximus*, therefore, is much more sensitive to the presence of mustard gas than man.[1] If *Limax maximus* is thus so extraordinarily sensitive to one gas, we have every reason for believing that it is extraordinarily sensitive to other gases, particularly those which emanate from its food substances such as fungi. If we assume such a sensitiveness, it is not difficult to imagine how it is that *Limax maximus* finds its way unerringly over a distance of many feet to the fruit-bodies of Phallus, Boletus, Russula, etc., which it devours with such avidity. The sense of smell in slugs, like that in dogs, is doubtless much more acute than in human beings.

Conclusions.—(1) The successful experiments with *Phallus impudicus*, *Russula heterophylla*, and *R. nigricans*, described above, clearly show that the fruit-bodies of these fungi, under certain conditions in the open, attract *Limax maximus* from a distance of at least 10 to 21 feet.

(2) Having regard to the well-known short-sightedness of slugs, to the fact that slugs find their food at night, and to the sensitiveness of *Limax maximus* to mustard gas when diluted to one part in ten million, my observations and experiments lead me to suppose that fungus-eating slugs react at a distance to the odours given off by fleshy fungi, and that in woods and gardens they find the fungi upon which they feed by their sense of smell.

(3) The chemotaxis of slugs, not merely for fungi but also for garden produce such as lettuce and cabbage, is a subject concerning which our information is still very meagre, but which is very amenable to experimental treatment. If the chemotaxis of slugs were sufficiently elucidated, we might perhaps be able to devise much more efficient means for protecting our gardens from the ravages of slugs than any at present known.

[1] Paul Bartsch, "Our Poison Gas Detector and How It was Discovered," Abstract of an Address delivered on February 7, 1920, to the Biological Society of Washington, U.S.A. I read a paper entitled "Upon the Chemotactic Attraction of Fungi for Slugs" at Chicago on December 30, 1920, before the Ecological Society of America. Subsequently Dr. R. F. Griggs called my attention to Dr. Bartsch's work, and then Dr. Bartsch kindly sent me an abstract of his Address.

CHAPTER IX

THE TYPES OF FRUIT-BODY MECHANISM IN THE AGARICINEAE

Introduction—The Characters of the Aequi-hymeniiferous or Non-Coprinus Type—The Characters of the Inaequi-hymeniiferous or Coprinus Type—The Characters of the Sub-types—Order of Description of the Sub-types—Order of Investigations

Introduction.—In Volume I of this work I distinguished between two general types of fruit-body organisation present in the Agaricineae: the Mushroom type, represented by *Psalliota campestris*, and the Coprinus type, represented by *Coprinus comatus*; and I endeavoured to make clear that both are admirably adapted to secure the successful production and liberation of the spores.[1] However, even in 1909, when preparing the first volume for the press, I felt that, before the organisation of hymenomycetous fruit-bodies could be thoroughly understood, it would be necessary to make a much more detailed examination of the arrangements of the elements of the hymenium in space and time than had hitherto been done. During the last thirteen years, I have attempted to secure the knowledge which was lacking, and have been successful far beyond my anticipations. What seemed at first, in the Mushroom type of fruit-body, to be but an irregular crowd of basidia with no very definite arrangement among themselves in regard to relative position and succession in time, has now been found in many species to be a wonderful army marching forward in well-spaced ranks; whilst a renewed investigation of the Coprinus type of fruit-body has revealed the fact that the basidia are dimorphic, the two kinds being interspersed among one another and packed together so as to form a beautifully efficient mosaic work. These and other facts of hymenial organisation will be laid before the reader in this and succeeding Chapters.

[1] Vol. i, 1909, pp. 210–214.

A comparison of the structure of the hymenium in a considerable number of Agaricineae has shown that each of the two general types of fruit-body organisation is made up of several sub-types. Now the Common Mushroom belongs to one of the sub-types. In order to avoid confusion, therefore, it has been found necessary to discard the term " Mushroom type " for one of the two generalised types and to adopt a more precise nomenclature. The first of the generic types, which includes all Agaricineae with the exception of the Coprini, will be called the *Aequi-hymeniiferous* or *Non-Coprinus Type*, and the second, which includes the species of the genus Coprinus only, will be called the *Inaequi-hymeniiferous* or *Coprinus Type*. The term *aequi-hymeniiferous* refers to the fact that the hymenium of the fungi belonging to the first type develops in an *equal* manner all over the surface of each gill both previously to, and during the period of, spore-discharge; whilst the term *inaequi-hymeniiferous* indicates that the hymenium of the fungi belonging to the second type develops in an *unequal* manner. The basidia in an inaequi-hymeniiferous hymenium develop and shed their spores in zones: a zone of spore-development, followed by a zone of spore-discharge, passes from below upwards on each gill. The Sub-types have been named after representative genera and species. A full list of the Types and Sub-types of fruit-body organisation which I have been able to distinguish is as follows:

ORGANISATION OF SPOROPHORES

I. The Aequi-hymeniiferous or Non-Coprinus Type

Includes all Agaricineae except Coprini.

A. The *Armillaria* Sub-type.
Examples: *Armillaria mellea, Collybia velutipes, Russula cyanoxantha, Pluteus cervinus, Nolanea pascua.*

B. The *Bolbitius* Sub-type.
Examples: *Bolbitius flavidus, B. titubans.*

C. The *Inocybe* Sub-type.
Examples: *Inocybe asterospora, Galera tenera.*

D. The *Panaeolus* Sub-type.

Examples : The species of *Panaeolus*, *Stropharia*, *Psilocybe*, and *Psalliota*.

E. The *Psathyrella* Sub-type.

Examples : *Psathyrella disseminata*, *Lepiota cepaestipes*.

II. The Inaequi-hymeniiferous or Coprinus Type

Includes all the species of the genus Coprinus.

A. The *Comatus* Sub-type.

Examples : *Coprinus comatus*, *C. sterquilinus*.

B. The *Atramentarius* Sub-type.

Examples : *Coprinus atramentarius*, *C. narcoticus*, and *C. macrorhizus*.

C. The *Lagopus* Sub-type.

Examples : *Coprinus lagopus* (= *C. fimetarius*), *C. domesticus*.

D. The *Micaceus* Sub-type.

Example : *Coprinus micaceus*.

E. The *Curtus* Sub-type.

Example : *Coprinus curtus*.

F. The *Plicatilis* Sub-type.

Example : *Coprinus plicatilis*.

We shall now pass on to a brief preliminary account of the two general types.

The Characters of the Aequi-hymeniiferous or Non-Coprinus Type.—These characters, which, of course, are those common to all the Sub-types included in the Type, are few in number. They may be described as follows :

(1) *Shape of the Gills.* All fruit-bodies belonging to the Aequi-hymeniiferous Type possess gills which are shaped like the blade of a pen-knife. The thickest part of each gill is attached to the pileus-flesh, whilst the sharp free edge is directed downwards toward the earth. The sides of the gills, therefore, are not parallel but are inclined to one another at an angle of a few degrees. A cross-section of a gill has a wedge-shaped appearance.

(2) *Geotropism of the Gills.* In addition to being wedge-shaped in cross-section, the gills of fruit-bodies of the Aequi-hymeniiferous Type are sensitive to the stimulus of gravity. During development they are positively geotropic, and they grow in such a way that their median planes are brought into vertical positions. If the pileus, after becoming expanded, is tilted through an angle, so that its orientation is permanently altered, in a short time the gills exhibit a reaction to the stimulus of gravity: they execute a turning movement about their lines of attachment to the pileus-flesh until at least their lower parts have become vertical again. The success of the re-adjustment depends upon the age of the gills and their angle of tilt. The younger the gills and the less the angle of tilt, the greater is the success which the gills attain in bringing their median planes into a vertical position.[1]

(3) *Position of the Hymenium in Space.* Owing to the fact that in the Aequi-hymeniiferous Type of fruit-body the gills are wedge-shaped in cross-section and positively geotropic, it follows that every part of the hymenium covering the gills in a normally oriented fruit-body comes to look more or less downwards toward the surface of the earth.

(4) *Development of the Hymenium.* The Aequi-hymeniiferous Type of fruit-body, as its name implies, bears a hymenium which develops in an approximately equal manner all over the surface of each gill: every small area of the hymenium (say every square mm.) on every gill of a fruit-body produces and liberates spores simultaneously during the whole of the spore-discharge period. On each small hymenial area, the basidia come to maturity and shed their spores in succession, so that the production and liberation of spores frequently continue for a period of several days.

(5) *Discharge of the Spores.* It was shown in Volume I that the spores of the Hymenomycetes are shot out more or less horizontally from the hymenium to a distance of 0·1–0·2 mm. and that, after being shot this distance, they curve in their trajectory sharply downwards and subsequently fall slowly in a vertical direction until they emerge from the interlamellar spaces into the outer air, whence they may be carried away from the

[1] *Cf.* vol. i, 1909, pp. 50–52.

fruit-body by the wind.[1] In the Aequi-hymeniiferous Type of fruit-body, correlated with the facts (*a*) that the hymenium everywhere looks more or less downwards toward the earth, (*b*) that the hymenium develops everywhere in an even manner, and (*c*) that the spores are shot a short distance perpendicularly away from the hymenium, we have the fact (*d*) that every small area of the hymenium (every square mm.) discharges spores successfully, *i.e.* so that they can escape from the fruit-body, during the whole period of spore-discharge.

(6) *Persistence of the Gills.* During the discharge of the spores, the gills are not dissolved by any process of autodigestion: they only begin to decay when the period of spore-discharge has come to an end.

(7) *The Pileus-flesh.* This is relatively thick and in large fruit-bodies often massive. It holds the gills in a fixed position during the whole period of spore-discharge, which in some species has a length of several days and in others of more than a week.

The Characters of the Inaequi-hymeniiferous or Coprinus Type.—Here, again, the characters are few in number and are common to all the Sub-types included in the Type. They may be described as follows:

(1) *Shape of the Gills.* The gills are parallel-sided or subparallel-sided. The gills are also relatively thin, so that their substance is often reduced to a minimum.

(2) *Ageotropism of the Gills.* The gills of the Coprini, unlike those of Type I, do not respond to the stimulus of gravity. They are brought into approximately vertical positions through a negatively geotropic reaction of the stipe.

(3) *Position of the Hymenium in Space.* Owing to the gills being parallel-sided, ageotropic, and often slightly wavy, under natural conditions one side of a gill often looks slightly upwards and the opposite side slightly downwards.

(4) *Development of the Hymenium.* The Inaequi-hymeniiferous Type of fruit-body, as the name implies, bears a hymenium which develops in an unequal manner on different parts of each gill. The basidia develop their spores in succession from below upwards

[1] Vol. i, 1909, pp. 184–189.

on each gill. The most advanced basidia are always at the lower free edge of each gill, while the least advanced basidia are always at the upper fixed edge of each gill. Each small area of the hymenium (one-tenth of a square mm.) does not produce a number of successive generations of spores, but all the basidia on the area come to have ripe spores upon their sterigmata almost simultaneously.

(5) *Discharge of the Spores.* The spores in the Inaequi-hymeniiferous Type of fruit-body are discharged in succession from below upwards on each gill. A zone of spore-discharge moves slowly from the lower edge to the top of each gill. The spores are shot more or less perpendicularly outwards from the hymenium in the zone of spore-discharge into the interlamellar spaces, and they then fall down slowly between the lamellae and escape in the same manner as in the Aequi-hymeniiferous Type.

(6) *Autodigestion of the Gills.* As the zone of spore-discharge moves from below upwards on each gill, it is followed very closely by a zone of autodigestion which completely destroys those parts of the gills which have become spore-free. The zone of auto-digestion, therefore, moves slowly from below upwards on each gill and eventually destroys the whole of each gill.

In Volume III, in which the development of various Coprini is treated of in detail, I shall endeavour to show that the ripening and discharge of the spores from below upwards on each gill and the autodigestion of each gill from below upwards are correlated with the successful liberation of the spores from parallel-sided ageotropic gills.

(7) *The Pileus-flesh.* This is relatively thin, even in large fruit-bodies. It becomes involved along with the gills in the process of autodigestion and is therefore destroyed centripetally. In consequence of this, in larger fruit-bodies, drops of a dark fluid—the products of autodigestion—are often to be observed hanging from the pileus-rim when the period of spore-discharge has become well advanced.

The two general Types of fruit-body organisation will be compared and contrasted after the Sub-types have been described in detail.

The Characters of the Sub-types.—The Sub-types of Type I are based almost solely on differences in the structure and arrangement

of the basidia and paraphyses, whilst those of Type II are based chiefly on the structure and arrangement of the basidia and cystidia, and upon the mode of expansion of the pileus. Each Sub-type is more or less different from the other Sub-types in the organisation of its fruit-body as a whole for the successful production and liberation of the spores. The exact nature of the Sub-types will be best realised when they are described in connection with specific fungi included in them. These descriptions will therefore not be given in this place but in succeeding Chapters in this volume and the next.

Order of Description of the Sub-types.—The Sub-types of Type I, already given on a previous page, are supposed to be arranged in order of increasing complexity; but this order will not be kept in the following Chapters. I have thought it best to describe Sub-type D, the Panaeolus Sub-type, first. This has been done because it is a very common clear-cut Sub-type and has been investigated by me in great detail. When the reader has read the description of this Sub-type, he will have but little difficulty in understanding the other Sub-types of Type I, although some of them will be dealt with much less fully.

Order of Investigations.—Having realised that, in the Agaricineae, the successive development of the basidia, which results in the discharge of a continuous stream of spores often for many days, is a striking phenomenon calling for detailed investigation, I determined to make a careful study of the hymenium of the Common Mushroom (*Psalliota campestris*). After the work upon this species was begun, a number of points were elucidated including the fate of the exhausted basidia. By examining very thin surface sections of the gills without immersing them in water, it was found that basidia which have discharged their spores can be recognised by the remains of their sterigmata, for these persist in the form of tiny stumps. However, the difficulty of finding out whether or not the hymenium contains paraphyses—special sterile elements—soon came to the fore. Then, having observed that the hymenial elements of the Mushroom are very small compared with those of many other Agaricineae, I came to the conclusion that the Mushroom was not a good starting-point for

my investigations. Following the advice of Polonius: "By indirections find directions out," I therefore left the Mushroom for a time and turned my attention to the Coprini. Here the elements of the hymenium in many species are relatively large and, excluding cystidia which may or may not be present, consist of definite and easily distinguishable fertile basidia and sterile paraphyses. By observing the autodigestion of the gill-edge, I was able to convince myself that the paraphyses in the Coprini are not young basidia and never develop into them, but are destined from the first to remain barren. I then passed on to the study of the fruit-body of *Panaeolus campanulatus*, which is organised in the same manner as that of *Psalliota campestris* but which has relatively much larger hymenial elements. The first phenomenon which attracted my attention in this species was the mottling of the gills. Its elucidation led to a complete understanding of the organisation of the elements of the hymenium. The relations of the basidia to one another in time and space were satisfactorily determined, the existence of paraphyses proved, and a mode of distinguishing the paraphyses from the basidia worked out. For the first time, complete surface views and cross-sections of the hymenium were drawn in which the nature and state of development of every element were recorded. The hymenium of *Stropharia semiglobata* was found to have a structure and mode of functioning just like that of *Panaeolus campanulatus*. The hymenium of the Mushroom (*Psalliota campestris*) was subsequently re-examined, and it was then easily discovered that its organisation is exactly similar to that of Panaeolus and Stropharia. Further investigations into the structure of the hymenium of species of Collybia, Bolbitius, Galera, Pluteus, etc., led to the recognition of the full list of Sub-types included within the Aequihymeniiferous or Non-Coprinus Type. An examination of about thirty species of Coprinus, some twenty of which were grown in the laboratory, revealed the Sub-types included within the Inaequi-hymeniiferous or Coprinus Type.

We are now in a position to pass on to the study of the organisation of the fruit-body of *Panaeolus campanulatus* which, in the next Chapter, will serve as an illustration of the Panaeolus Sub-type.

CHAPTER X

THE AEQUI-HYMENIIFERAE: THE PANAEOLUS SUB-TYPE ILLUSTRATED BY PANAEOLUS CAMPANULATUS

The Panaeolus Sub-type—*Panaeolus campanulatus*: General Remarks on the Sporophore—The Phenomenon of Mottling—The Spore-fall Period—Apparatus and Method for Observing the Development of the Hymenium—Observations on the Developing Hymenium—Successive Generations of Basidia—Description of the Hymenium of *Panaeolus campanulatus* in Detail—Significance of the Development of the Basidia in Successive Generations on any One Hymenial Area, and of the Existence of Various Areas—The Spores which are Wasted—Significance of the Protuberancy of Mature Basidia—Significance of the Collapse of Exhausted Basidia—The Relative Position of the Basidia and the Spores of One Generation—The Position of the Sterigmata in the Hymenomycetes generally and in *Panaeolus campanulatus*—The Cheilocystidia.

The Panaeolus Sub-type.—The Panaeolus Sub-type of fruit-body organisation possesses all the general characters already described for the Aequi-hymeniiferous Type: the gills are wedge-shaped in cross-section and positively geotropic, the hymenium looks downwards to the earth, and every part of the hymenium produces and liberates spores during the whole period of spore-discharge.

The most striking of the special characteristics of the Panaeolus Sub-type is that the hymenium is made up of a mosaic-work of small, irregular, local areas. In some of these the spore-bearing basidia are relatively advanced in that they are approaching the climax of their development which ends in spore-discharge and collapse, whilst in others the spore-bearing basidia are relatively young as is shown by the fact that the spores on their sterigmata are very immature. In species with pigmented spores—and these alone have so far been found to belong to the Panaeolus Sub-type—owing to the fact that the pigment is produced during the second

half of the development of each spore, the hymenial mosaic-work is *mottled*. The mottling can be seen with the naked eye. The areas with the more advanced spore-bearing basidia are relatively dark, and the areas with the less advanced spore-bearing basidia relatively light. The basidia in any small area of the hymenium come to maturity in a series of sharply defined successive generations. A dark area becomes a light area as soon as the spore-bearing basidia, which are approximately equal in their state of development, have shed their spores. The light area so produced remains light until the basidia of a new generation have advanced so far in development that their spores are beginning to be pigmented. The light area then turns dark again. The alternation of darkness and lightness in an area continues until all the generations of basidia have come to maturity and the hymenium is exhausted. The spore-bearing basidia on any dark or light area are closely packed together side by side. All the basidia of the hymenium are *monomorphic*, *i.e.* when they reach maturity and are bearing spores they all project to an approximately equal distance beyond the general surface of the hymenium.

Mottling of the gills is a striking macroscopic colour-indication of the mode of organisation of the hymenium and, where it occurs, serves to distinguish the Panaeolus Sub-type from all the other Sub-types.

Panaeolus campanulatus: General Remarks on the Sporophore.—This species was chosen for detailed study for the following reasons. Its fruit-bodies (Fig. 83) possess hymenial elements sufficiently large for convenience of observation, black spores of considerable size (the three dimensions being 13–14 × 9 × 6–7 μ), and thin transparent gills. The fungus is coprophilous and can be easily cultivated from spores on sterilised horse dung. Upon this medium, at ordinary room temperatures, it can pass through the whole of its life-history from spore to spore in five weeks. By making artificial cultures in the laboratory I was able to obtain a constant supply of fruit-bodies all through the Manitoban winter—a period of severe frost, lasting five months, during which not a single fleshy agaric of any kind can be gathered in the open. The sporophores of *Panaeolus companulatus* are also of suitable size

for handling with such apparatus as it was desirable to use. Lastly, the gills exhibit in a marked manner the phenomenon of mottling, which had not hitherto been investigated (Fig. 84).

The material was obtained in the first place from England.

Fig. 83.—*Panaeolus campanulatus.* Three fruit-bodies grown on horse dung in a pure culture in the laboratory. Natural size.

In the month of August, 1911, some horse dung infected with the mycelium of *Panaeolus campanulatus* was procured from a field and allowed to dry. Subsequently it was taken to Winnipeg, where in February, 1912, *i.e.* some six months after it had been dried, it was again moistened. The wetted dung-balls were placed in a large crystallising dish, which was covered with a glass plate to check evaporation and set upon a table in the laboratory.

A few weeks after the culture had been started, a fruit-body of *Panaeolus campanulatus* came up, and on March 6 it was found to be shedding spores. On that day some fresh horse-dung balls were placed in a crystallising dish, 7 inches in diameter and 2 inches high, and covered with a glass plate. They were then sterilised by heating for half an hour at 100° C. in a steam steriliser. As soon as the culture was sufficiently cooled, the glass cover was raised, and the dung-balls were infected by rubbing their surfaces with the gills of the Panaeolus. This operation was performed in a few seconds with the aid of sterilised forceps. The resulting culture, which was kept at room temperature, was practically pure : the mycelium grew not only inside the dung-balls but over their surface. The first fruit-body was observed to be coming up on the thirty-first day after the culture had been started, and on the thirty-fourth day it began to shed its spores. A number of other fruit-bodies were subsequently produced, and fresh cultures were made from them from time to time as occasion required.

The general appearance of the fruit-bodies of *Panaeolus campanulatus* is shown in Fig. 83, while vertical sections are shown in Figs. 84 and 87. The pileus is usually conico-campanulate (Fig. 84), but under very moist conditions may become considerably expanded although never quite flat (Fig. 87). The fruit-body shown in section in Fig. 87 was grown in the laboratory under very moist conditions, and exhibits the extreme amount of expansion which has so far been observed. A comparison of fruit-bodies found in grassy fields and of fruit-bodies cultivated in the laboratory has convinced me that there is usually greater expansion in the latter. Probably this is due to the fact that, under the artificial conditions, transpiration is hindered and the pileus-flesh is thereby supplied with much more moisture than under natural conditions. The pileus is rufescent under natural conditions, but fruit-bodies reared in the laboratory appeared brownish or light leather-colour and were certainly much less rufescent than I have seen them in nature. The top of the pileus is smooth and, in moist weather, somewhat viscid. The flesh is well developed, especially at the disc.

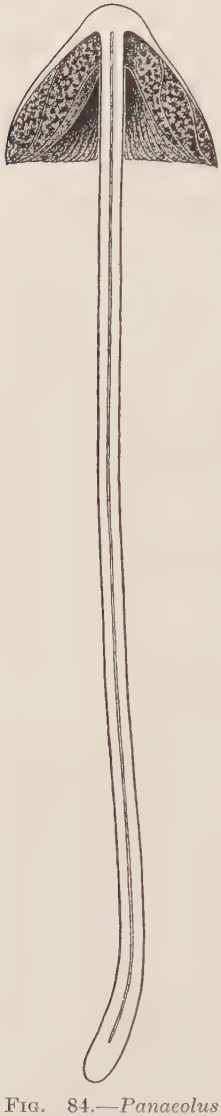


Fig. 84.—*Panaeolus campanulatus*. A vertical section of a fruit-body found growing wild on horse dung in a field at King's Heath, England. The mottling of the gills is well exhibited. Natural size.

The gills are adnate to the stipe, rather broad in the middle, and, when the pileus becomes very expanded, have a tendency to break away from the stipe. This breaking away, however, does not occur in typical campanulate pilei. The sides of the gills are mottled grey and black in a very conspicuous manner. The edges of the gills are white. This is due to the presence of what we may call *cheilocystidia*, *i.e.* hair-like structures which form a fringe along the gill-edge. These cheilocystidia excrete mucilage at their tips, often in considerable quantity. The mucilage belonging to adjacent hairs often becomes confluent, and thus forms balls of mucilage of considerable size, the larger of which with the microscope may be seen clinging to as many as twenty different hairs. These balls of mucilage, in fruit-bodies growing on dung in fields, often occur at close intervals all along each gill-edge, and are not infrequently sufficiently large to be observed with the naked eye. A more detailed description of the cheilocystidia and their excretory products will be reserved until we approach the end of the Chapter.

The characters which belong to the Aequihymeniiferous Type of fruit-body organisation are well developed in *Panaeolus campanulatus*. The gills, as is shown in Fig. 85, although rather thin, are wedge-shaped in cross-section. They are also positively geotropic and have their sharp edges directed toward the ground. Consequently, the hymenium everywhere looks more or less downwards. Every small area of the hymenium (every square mm.) produces and liberates spores during the whole period of spore-discharge. This is indicated in our

Figure by the arrows which mark the trajectories of a number of spores which have been shot away from the hymenium in various parts of the gills almost simultaneously.

The spores in *Panaeolus campanulatus* are shot from their basidia straight forward for a distance of about 0·1 mm. (Fig. 85). The basidia in the hymenium on the sides of the gills have the axes of their bodies and of their sterigmata almost horizontally situated, and they therefore project their spores in a more or less horizontal direction straight outwards from the gills into the interlamellar spaces. In still air, as I have shown in Volume I, the projection-velocity of any discharged spore is almost instantly reduced to zero, so that a spore, after travelling horizontally a distance of about 0·1 mm., turns sharply downwards through a right angle and then falls vertically toward the earth. I have called the peculiar trajectory described by a spore a *sporabola*.[1] The steady terminal rate of fall of the spores of *Panaeolus campanulatus* in still air is from 2 to 3 mm. per second.[2]

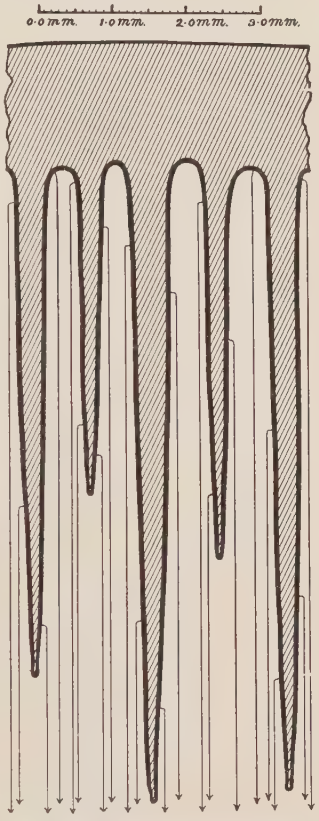


Fig. 85.—*Panaeolus campanulatus*. A vertical section through the pileus-flesh and several gills showing shape and direction of gills. The trajectories of a number of spores in still air are indicated by the arrows. Magnification, 20.

The interlamellar spaces, although less than one millimetre wide between any two adjacent gills (as may be seen by reference to the scale in Fig. 85), are sufficient to permit of the escape of all the spores when the fruit-body is oriented in a normal manner, *i.e.* when the end of the

[1] Vol. i, 1909, Chap. XVII, p. 185.

[2] For *Panaeolus campanulatus*, the exact horizontal distance of spore-discharge and the exact rate of fall in still air have not been measured. The estimates given above are based on measurements made for a considerable number of other species having spores of various sizes. *Cf.* vol. i, pp. 142 and 175.

FIG. 86.—*Panaeolus campanulatus*. The gills from about one-sixth of a pileus, drawn in succession. Natural size.

stipe has its axis vertical and the pileus with its gills is symmetrically situated upon it. The two deepest gills shown in Fig. 85 are gills which, when seen in lateral view, stretch from the stipe to the periphery of the pileus, while the three gills of lesser depth are not attached to the stipe and therefore have a shorter length (*cf.* Fig. 87).

The outlines of forty-two successive gills which were removed from about one-sixth of a small pileus are shown in Fig. 86. The gills naturally fall into three classes: (1) long gills which extend from the stipe to the periphery of the pileus, (2) gills of medium length which extend only a part of this distance, and (3) short gills which are present only at the pileus margin. The two deepest gills and the three gills of lesser depth in Fig. 85 evidently correspond respectively to the long gills and gills of medium length in Fig. 86. The total number of gills in the small fruit-body from which the forty-two gills were removed was about 240, and the hymenial area supported by all the gills together was estimated to be about 88 square centimetres.

A fruit-body usually begins its development toward the base of a dung-ball, to which it becomes firmly attached by an extension of the base of the stipe in the form of a gelatinous layer or mass (Figs. 83 and 87). The stipe, on beginning to elongate, is ageotropic but positively heliotropic: it therefore grows towards the light. The pileus at this stage is small, hard, and conical, so that it can be pushed with relative ease by the heliotropic stipe past obstacles into the open. After the pileus has been brought into the open, the apical portion of the stipe becomes strongly negatively geotropic and ceases to respond to the stimulus of light. The stipe, therefore, as it completes its elongation, grows vertically upwards; and, since the pileus is attached to the stipe-apex in

a radially symmetrical manner, the axis of the pileus becomes perpendicular. The bringing of the median planes of the gills into exactly vertical positions is accomplished by two adjustments, a coarse and a fine. The coarse adjustment consists of the already mentioned negatively geotropic movement of the apex of the stipe which brings all the median gill-planes into approximately vertical positions. The fine adjustment, by which these planes are brought precisely into vertical positions, is accomplished by the gills themselves, for these become positively geotropic and grow downwards toward the earth's centre.[1]

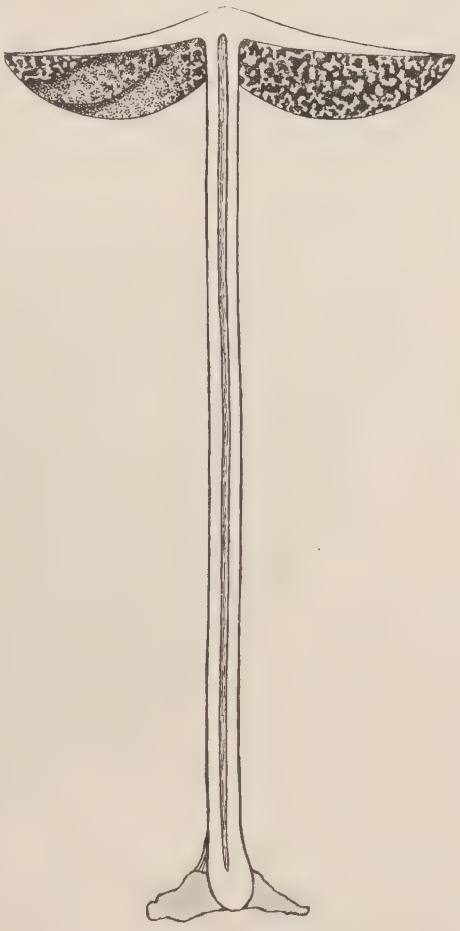


Fig. 87.—*Panaeolus campanulatus.* Section of a fruit-body to show the mottling of the gills. In the dark areas of the gills, the basidia bear black spores which are ripe or nearly ripe. In the light areas the basidia bear immature spores which are either colourless or are only beginning to turn brown. The base of the hollow stipe is attached to a brown gelatinous layer of mycelium. Grown in a pure horse-dung culture from spores obtained from a fruit-body of English origin. The pileus is expanded more than is usual under natural conditions (*cf.* Fig. 83). Natural size.

The Phenomenon of Mottling.—When the surface of a gill of *Panaeolus campanulatus* which is shedding spores is observed with the naked eye, one can at once distinguish upon it a considerable number of lighter and darker areas which are so arranged as to give the hymenium a mottled appearance (Figs. 87 and 88). These areas, of which the larger ones measure 1–2 mm. across, are of very

[1] *Cf.* vol. i, 1909, p. 49.

unequal size and of the most diverse shapes. In their totality, therefore, they do not give rise to any regular pattern. It is also to be remarked that the mottling on one side of a gill does not correspond with that on the other: the opposing hymenial areas develop quite independently of one another. One rule, however, appears to hold, namely, that the sum of the darker

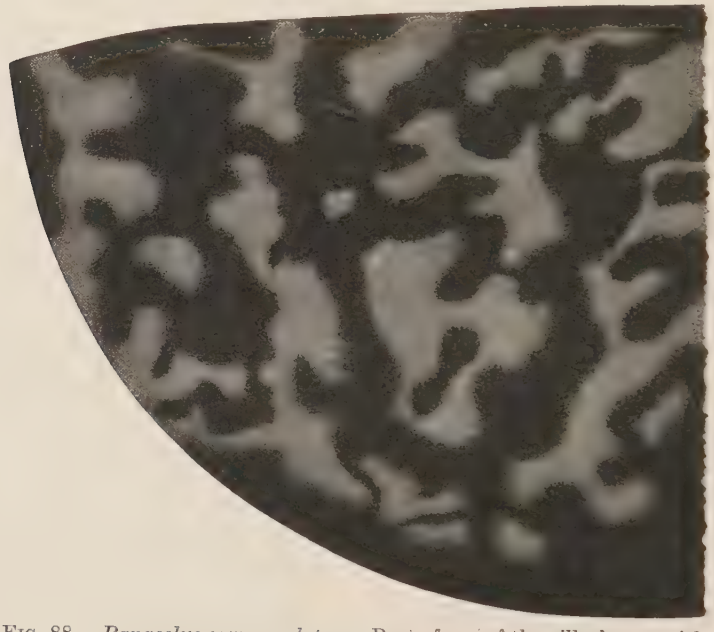


FIG. 88.—*Panaeolus campanulatus.* Part of one of the gills drawn with a *camera lucida* to show the mottling of the hymenium. In the darker areas the basidia bear black spores which are nearly or quite mature. In the lighter areas the basidia bear spores which are either colourless or are only beginning to turn brown. Magnification, about 10.

areas always exceeds by a considerable margin the sum of the lighter areas (*cf.* Fig. 88). For this rule a good explanation will be forthcoming when we have studied the development of one small portion of the hymenium.

Mottling of the gills is one of the most obvious field-characters of the Panaeoli. Indeed, the generic name *Panaeolus*, which we owe to Fries,[1] was chosen on this account: it is derived from the Greek word *panaiolos* meaning *all-variegated* or *mottled*. The

[1] E. Fries, *Epicrisis*, Upsaliae, 1836–38, p. 234.

species of Panaeolus, which have an annulus on their stipe after the expansion of the pileus, were separated from their fellows by Karsten [1] and included in a new genus *Anellaria*, so that we now have two genera of black-spored Agaricineae with mottled gills. The other genera included in the Melanosporae are Coprinus, Psathyrella, and Gomphidius. In the first two mottling is absent, owing to the fact that the hymenial elements are arranged in a very different manner from those of Panaeolus and Anellaria. Whether or not there is any trace of a fine mottling on the gills of the species of Gomphidius remains to be investigated.

Mottling of the gills is by no means confined to certain of the genera of the Melanosporae, although it is most noticeable in them owing to the fact that the spores are black and the lighter and darker areas often relatively large. Among the Porphyrosporae, where the spores are purple, brownish-purple, or dark brown, I have observed the phenomenon in Psilocybe, Hypholoma, Stropharia, and Psalliota, and among the Ochrosporae, where the spores are yellow-brown or rust-colour, in Flammula, Cortinarius, Crepidotus, and Pholiota. It is not asserted that *all* the species belonging to these genera have mottled gills, for my investigations so far are not sufficiently extended to make any such sweeping generalisation; but that each genus named has at least some species in it with mottled gills I cannot doubt. The Table on page 254 is a list of some of the species in which mottling of the gills has been observed.

Of Rhodosporae I have carefully examined *Pluteus cervinus* and *Nolanea pascua*. These certainly do not belong to the Panaeolus Sub-type and, both macroscopically and microscopically, show not a trace of mottling. I have also not been able to observe mottling with the naked eye on the gills of *Entoloma prunuloides*. The evidence so far collected, therefore, indicates that the Rhodosporae, as a group, have their hymenium very differently organised from that of the Panaeolus Sub-type. The hymenial organisation for the production and liberation of spores in *Pluteus cervinus* and *Nolanea pascua* is, as we shall see, quite similar to that in

[1] P. A. Karsten, *Rysslands, Finlands och den Skandinaviska Halföns Hattsvampar*, Helsingfors, 1879, p. 517.

many Leucosporae, such as species of Armillaria, Collybia, and Marasmius.

Species of Agaricineae having Mottled Gills.

Melanosporae	Panaeolus campanulatus
	,, papilionaceus
	Anellaria separata
Porphyrosporae	Psilocybe ericaea
	.. foenisecii
	.. semilanceata
	Hypholoma fasciculare
	,, velutinum
	,, pyrotrichum
	Stropharia semiglobata
	.. aeruginosa
	Psalliota campestris
	,, arvensis
	,, silvatica
Ochrosporae	Cortinarius arvinaceus
	.. collinitus
	Crepidotus mollis
	Flammula carbonaria
	Pholiota mutabilis

If the spores of a Panaeolus were colourless instead of black, the underlying organisation of the hymenium would not be altered : it would simply be more difficult to detect. The areas with more advanced spore-bearing basidia would be light in colour just like the areas with less advanced spore-bearing basidia, and one would not be able to observe the difference by the appearance of the exterior of the spores. In order to discover the mosaic-work really present, it would be necessary to watch the development of the hymenium for a considerable number of hours directly with the microscope. Now, in the Leucosporae, the spores are colourless, and the question arises whether any of the species in this very large family have the hymenial organisation characteristic of the Panaeolus Sub-type. Examination of a number of

Leucosporae has convinced me that many of them do not have this organisation but some other different from it, and I have so far not been able to find any white-spored species belonging to the Panaeolus Sub-type. Among Leucosporae which certainly do not belong to this Sub-type may be mentioned species of Marasmius, Collybia, Armillaria, and Russula. It must be admitted, however, that my investigations have not yet been sufficiently extended to warrant the conclusion that the Panaeolus Sub-type does not contain any species with colourless spores. Only further research can decide this matter.[1]

In some of the species named, *e.g. Psilocybe foenisecii* and *Stropharia semiglobata*, if the fruit-bodies are in good condition, the mottling is almost as obvious as in the Panaeoli, but in other species, *e.g. Psalliota campestris*, the Common Mushroom, the phenomenon would certainly be overlooked unless one observed the surface of the gills closely. Here the mottling has a fine texture, but can easily be made out with the naked eye when one's attention has been turned to it.

In order to investigate the organisation of the hymenium in *Panaeolus campanulatus*, a gill was removed from a fruit-body grown in the laboratory, laid flat on a glass slide, and covered with a large cover-glass. No mounting fluid was used. Under these conditions the gill, protected as it was by the cover-glass from rapid loss of water, remained living for a long time. The cover-glass touched the upper hymenium only at a few places, so that most of the hymenial elements were left undisturbed.

On examination of the upper surface of a living gill under the conditions described, the immediate cause of the mottling can be readily determined. In a black area, a large number of basidia are in almost precisely the same state of development: they each bear four black or blackening spores and are so spaced that the

[1] It is possible that the Panaeolus arrangement of basidia exists in the large fruit-bodies of *Lepiota procera* (vol. i, Figs. 14 and 15, pp. 44 and 45). In this species, as in Panaeolus, I observed that the basidia are monomorphic, that the basidia which bear spores are rather closely packed together, and that here and there on the hymenium small groups of basidia can be seen in which all the spores are not yet of full size and therefore are very young; but, up to the present, I have not been able to complete this investigation.

spores of adjacent basidia cannot touch one another. Basidia bearing partly-grown and colourless spores are absent. Such a black area is illustrated in the middle of Fig. 89, which shows the result of a *camera-lucida* drawing in which all the spores were sketched. In a white area, just as in a black, there are a considerable number of spore-bearing basidia, which are separated from one another by such distances as to prevent the spores of adjacent basidia from ever coming into contact (Fig. 89) and which are all of about the same age ; but here the spores are only partially grown or, if full-grown, colourless or here and there showing but a faint tinge of brown. It is evident that the black and the white areas owe their appearance to the amount of pigment in the spores present on each : in the black areas the spores are all black, while in the white areas the spores are colourless. Now the colour and the state of development of any spore are correlated, for a spore is always colourless when it is young, and only acquires pigment when it is nearing maturity. So far as their development is concerned, basidia bearing colourless spores are comparatively young, wh lst basidia surmounted with black spores are comparatively old. We can therefore say that the generation of basidia bearing spores in a black area is older than the generation of basidia bearing spores in a white area.

From the observations just described it seemed to me safe to make the following deductions : (1) as the spores ripen, a white area must change into a black area, (2) the spores on a black area, since they are all of about the same age, must all be discharged at about the same time, (3) on discharge of its spores, a black area must turn into a white area, and (4) there must be areas intermediate between the black and the white.

On studying the hymenium again, I found no difficulty in observing the intermediate areas. A *camera-lucida* sketch showing black, white, and intermediate areas is given in Fig. 90. One can see from the drawing that, in the piece of hymenium represented, *waves of development* are exhibited. A large black area at *a* and *c* passes by means of two intermediate areas, in which the spores are turning brown, into two white areas at *b* and *d* respectively. In Fig. 89, the browning of some of the colourless spores,

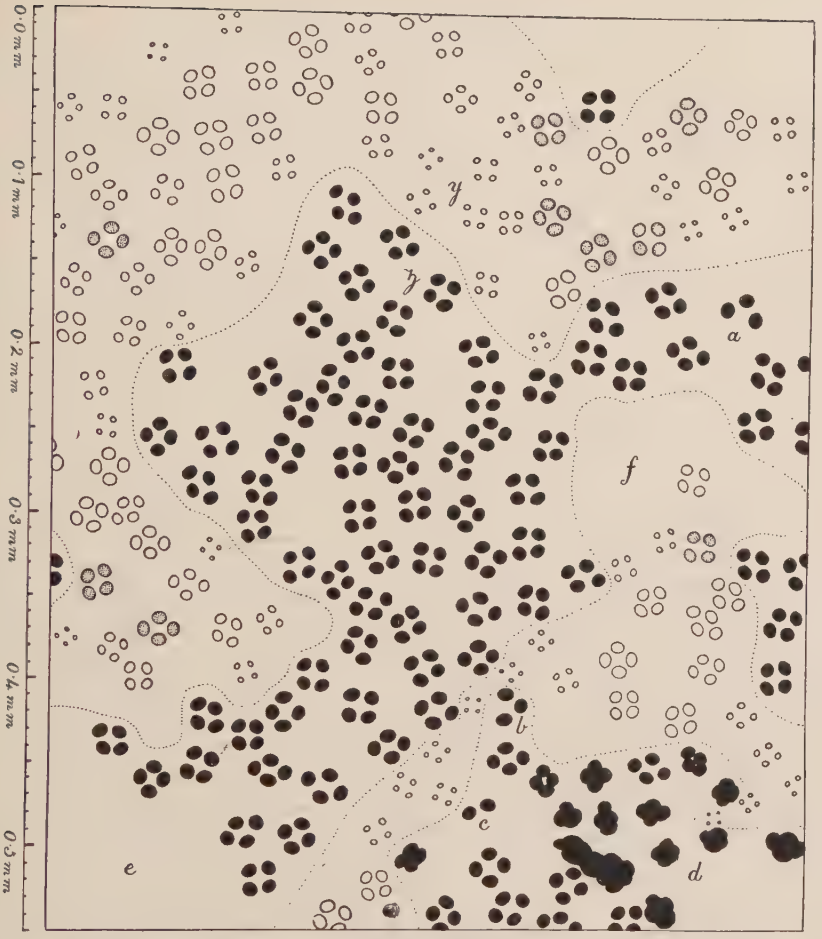


FIG. 89.—*Panaeolus campanulatus.* Part of the hymenium on the side of a gill, showing the spores only, sketched with the help of a *camera lucida* on the second day of spore-discharge. The dotted lines have been added in order to enable the eye to distinguish more readily the darker and lighter areas of the mottled hymenium. In the darker areas the spores are black, and either ripe or nearly ripe. In the lighter areas the spores are either colourless (unshaded) or are beginning to turn brown (shaded with dots). All the spores in the central dark area are of approximately equal age and will be shot away approximately at the same time. Another generation of basidia will then produce colourless spores in this area which will then be white; then, as the spores become pigmented, the area will gradually change from white through brown to black again. The white areas shown in the illustration are destined to turn black owing to the ripening of the spores; after the spores have been shot away, they will become white again. *y*, spores not 15 minutes old, rapidly developing in size; *z*, ripe spores shortly before discharge, about 9 hours old. At *a*, *b*, and *c*, the basidia have just discharged some of their spores. The heaps of spores at *d* were produced owing to excessive excretion of water from the sterigmata, which took place whilst the sketch was being made under very moist conditions. Had the conditions been normal, the basidia concerned would have discharged their spores into the air. The blank spaces at *e* and at the other corners of the drawing are due to the fact that the spores present in these areas were not sketched. In the blank space at *f*, several basidia have just discharged their spores: in this area the basidia of the next generation are completing the development of their sterigmata just prior to the production of spores. The area sketched = 0·25 square mm. Magnification, 220.

and therefore the beginning of the development of intermediate areas on the hymenium, is indicated by slight shading.

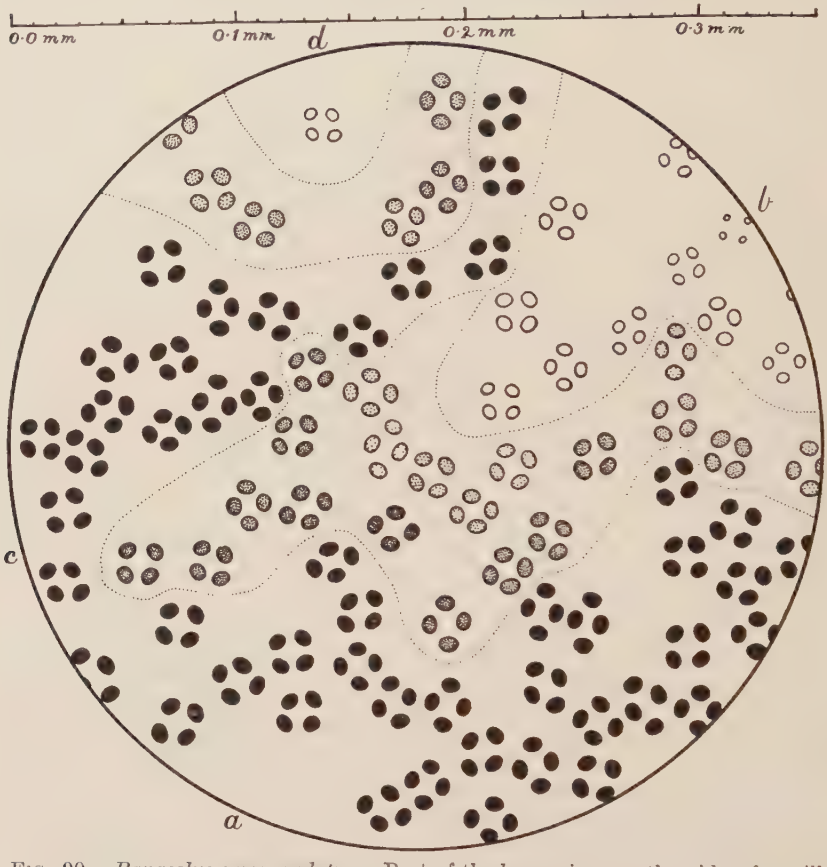


Fig. 90.—*Panaeolus campanulatus.* Part of the hymenium on the side of a gill, showing spores only, sketched with the help of a *camera lucida* on the first day of spore-discharge. The dotted lines have been added in order to enable the eye to distinguish more readily the black, white, and intermediate areas from one another. There are waves of development from *a* to *b* and from *c* to *d*. In the intermediate areas, the spores (shaded with dots) are turning from brown to black. The area shown = 0·1 square mm. Magnification, 300.

When two waves of development approach each other from opposite directions, the appearance of the hymenium may be like that shown in Fig. 89. Here two waves of development are advancing to the middle of the area from what we may call the south-east and north-west respectively. Although in the central black area all the spores are equally black, the ripest spores are

those situated next to the dotted contour lines and the least ripe those occupying the very middle of the drawing. For the black central area, therefore, the development and order of spore-discharge is centripetal.

A study of areas like those represented in Figs. 89 and 90 leads one to the conclusion that the hymenium of a gill of *Panaeolus campanulatus* is so organised that its development takes place in a series of waves of small dimensions, which move irregularly and simultaneously through it.

The Spore-fall Period.—By placing a series of pieces of white paper under the pileus of a large specimen of *Panaeolus campanulatus* growing upon horse dung under a bell-jar in the laboratory, and by observing the daily spore-deposits, it was found that the period of spore-fall lasted for eleven days. As judged by the blackness of the spore-deposits accumulated during each 24 hours, the rate at which spores were given off attained its maximum about the second or third day. Thereafter it slowly declined, fewer and fewer spores being shed each day. The spore-deposits for the first seven days were all fairly dense, those for the next three days very thin, and that formed on the last day only just recognisable. On the twelfth day the stipe collapsed. By means of a calculation, the details of which will be given in a subsequent section,[1] the total number of spores which were liberated during the whole spore-fall period was determined to be about 215,000,000. Some other fruit-bodies were observed to shed spores for at least a week.

From the above observations it is clear that the spore-discharge period lasts for a considerable number of days. Now if, during any of the days when spores are streaming from the pileus, one examines the hymenium of one of the gills, one observes that everywhere it exhibits basidia bearing spores. The Figs. 89 and 90 would do to represent the hymenium for any of the first four days of spore-discharge. From a consideration of these facts, one can make an important deduction : as soon as one generation of basidia on a black area has shed its spores, its place is at once taken by another generation of basidia, which rapidly develops

[1] The section called : " The Spores which are Wasted."

a new crop of spores. We are thus led to the supposition that, in all probability, *each area gives rise to a series of successive generations of basidia*. But a probability is a very different thing from a fact established by direct observation. In order to test the correctness of the deduction just brought forward, it seemed highly desirable to do what I believe has never before been attempted, namely, *to watch the changes taking place in one and the same piece of hymenium for several days*. Accordingly, some special investigations were undertaken which will now be described. We may here anticipate their result by stating that the test of direct observation has conclusively demonstrated the correctness of the idea of a series of successive basidial generations.

Apparatus and Method for Observing the Development of the Hymenium.—In devising the apparatus and method about to be described, the object aimed at was to observe the changes taking place in one small area of the hymenium under sufficiently normal conditions of development and for as long a time as possible.

A glass crystallising dish (Fig. 91, D), 5 inches in diameter and 2 deep, was stood on its side so that it rested on a wooden block (W) set on a stand (S) having a circular top. The dish was held in place by a vertical elastic band (VB). The fruit-body to be examined, together with the surface mycelium attached to the base of the stipe and a little of the substratum, was then removed from the culture dish, and with the aid of a sharp scalpel two parallel and vertical cuts were made through the pileus on each side of the stipe about one quarter of an inch apart. Two pieces of the pileus were thus removed. From one of the gill-bearing pieces of pileus still left attached to the stipe all the gills were dissected away except one, which thus being freed from its fellows afforded an admirable object for exact study. In general appearance it resembled the right-hand gill shown in Fig. 87 (p. 251). Immediately after being operated upon, the fruit-body was placed inside the crystallising dish in its natural position as shown in the accompanying Fig. 91, so that the gill to be examined (the one to the right) had its median plane vertically situated. The base of the stipe, together with the mycelium and horse dung attached to it, was then surrounded with wet cotton-wool (CW) held in position

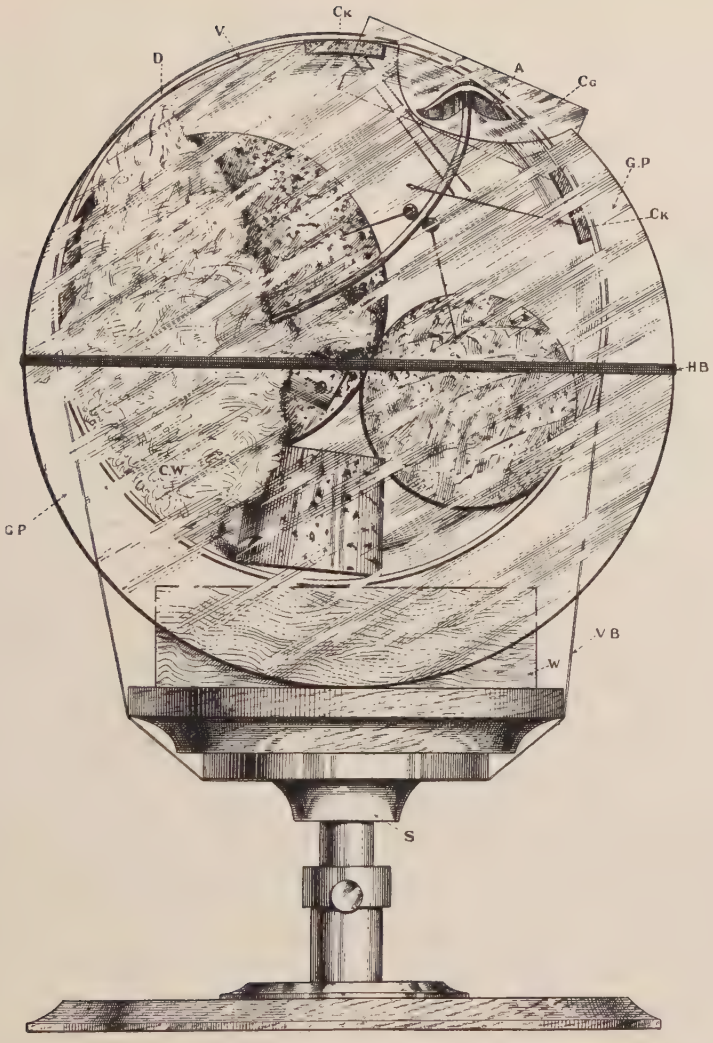


Fig. 91.—Apparatus for observing the development of successive generations of basidia and spores on a small portion of the hymenium of a gill of *Panaeolus campanulatus*. S, a circular stand made of brass and wood, on which is resting a block of wood, W. The glass dish, D, rests on the block, W, and is held in place by the elastic band, VB. The dish is closed in front with the exception of the small ventilating space, V, by the thick glass plate, GP, which rests on the top of the stand and is held to the glass dish by the horizontal elastic band, HB. The strip of thin cover-glass, Cg, is attached by a mixture of wax and fat to the inner surface of the glass plate at a place where part of the plate has been broken away. The dish is partly filled with three large corks. A fruit-body of *Panaeolus campanulatus* has been removed from a culture and placed in the dish so that the base of its stipe is covered by the wet cotton-wool, CW. The pileus, after being dissected so that only one gill is left on the right-hand side, rests against the side of the glass dish. The fruit-body is also fixed in a constant position by the three needles stuck in the strips of cork, Ck, and by the black-headed pins stuck into the two large circular corks. A is an area of the hymenium which was observed with a horizontal microscope for three days and three nights. Reduced to one-half the actual size.

by means of corks and pins. The pileus was prevented from altering its position by being placed in contact with the crystallising dish above; and the stipe was held by two black-headed pins fixed to the two large circular corks and by three darning needles coming from the pieces of sheet cork (Ck) which had been attached to the side of the dish by means of sealing-wax. A circular glass plate (GP), from which a piece of the glass had been removed at the edge, was then obtained. For the piece of glass broken away a very thin sheet of cover-glass (Cg) was substituted, the attachment to the inner side of the thick glass plate being effected with the aid of melted paraffin wax. The glass plate was then set in front of and against the crystallising dish, so as to close it, except for a small space (V) which was left for ventilation. The plate was arranged so that it rested on the stand (S) and so that the thin cover-glass (Cg) attached to its inner surface was opposite to the pileus. Slipping of the plate was prevented by a horizontal elastic band (HB) which passed around the back of the dish. After the plate-cover had been applied to the dish, the gill to be observed, shown on the right hand in Fig. 91, was about 2 mm. from the surface of the cover-glass.

The gill was observed with a horizontal microscope attached to a stand of simple construction, an instrument which had already been used to determine the rate of fall of spores (Fig. 92).[1] The tube of the microscope was raised to the requisite height by placing the stand on a wooden box, and was focussed by pushing the stand backwards and forwards and by means of a brass adjustment-screw. The tube-length was 130 mm. The ocular was No. 4 and the objective No. 3 of the Leitz system. The magnification was about 85 diameters and the field of vision 2 mm. in diameter. The position and extent of the hymenial area, the development of which was to be investigated with the microscope, are shown by the dotted circle A, in Fig. 91. The illumination of the hymenium was effected by light passing through the whole substance of the gill. Diffused sunlight was employed during the day and diffused electric light coming from strongly lighted white paper at night.

[1] *Cf.* vol. i, 1909, p. 167, and Plate IV, Fig. 29.

The fruit-body made use of for study, before being removed from the culture dish, had already been shedding spores for about 24 hours, so that, when it was first observed with the horizontal microscope, it was beginning its second day of spore-discharge. Its gills showed the usual mottling of lighter and darker areas so

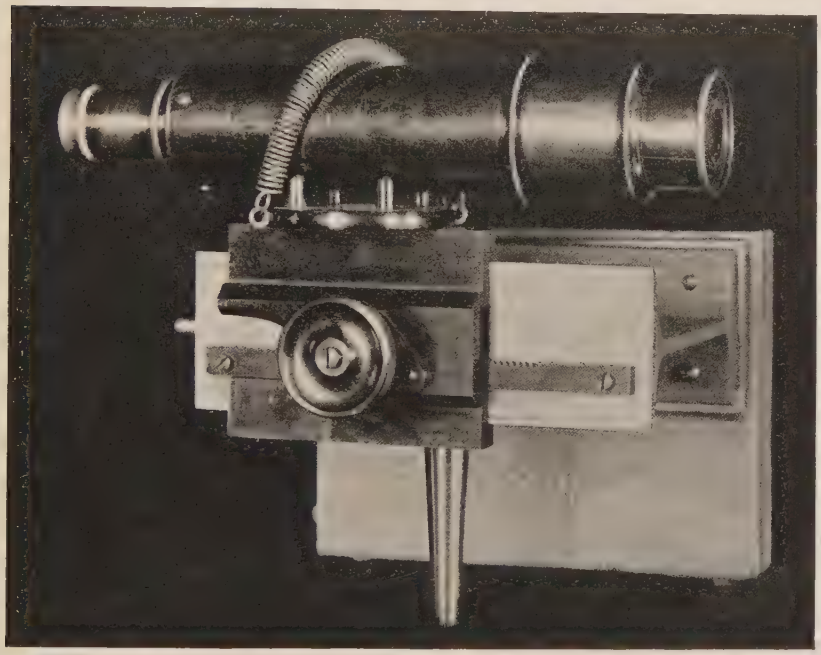


Fig. 92.—The horizontal microscope of simple construction used for observing the development of the hymenium in the area A of Fig. 91. About three-fifths the actual size.

characteristic for all species of Panaeolus. The gill watched with the horizontal microscope, whilst under observation, was subjected to conditions very similar to those in nature in that : (1) it had its normal orientation in space, (2) it remained attached to the pileus, and (3) it was surrounded with damp air at a medium temperature. Under these conditions the gill continued its development, and for three further days and nights continued to produce and liberate spores. It thus became possible for me to follow the development of one and the same piece of hymenium on a gill which was subjected to normal conditions for a considerable period of time.

One practical difficulty in observing the hymenium, and the manner in which it was overcome, may here be mentioned. At first, when the gill surface was focussed, the basidia and their spores could be clearly seen : their definition was sharp. However, it was soon found that the cover-glass (Fig. 91, Cg) often became fogged owing to the condensation upon it of water-vapour transpired from the pileus. When this fogging occurred, the hymenium seen through the microscope presented nothing but a blurred appearance. The removal of the water drops was readily effected with the aid of a darning needle. This was taken in a pair of forceps, heated for a short time in the flame of a spirit lamp, and then rubbed two or three times over the outer surface of the cover-glass. In a few seconds the film of moisture evaporated, and then the hymenium could be seen clearly again. As this clearing operation was always performed with care, the gill (the surface of which was about 2 mm. distant from the cover-glass) was never injured or its continuous development disturbed.

Observations on the Developing Hymenium.—The horizontal microscope was at first moved about in front of the gills to be observed until the middle of its field came to include what might be termed a black island, *i.e.* a black area of the hymenium very much resembling that in the centre of Fig. 89 (p. 257) but practically surrounded by a white area. This black area, upon which my attention became concentrated, was about 1 mm. wide, and had a peculiar outline by which it could be recognised again after any break in observation. Its sole spore-bearing elements consisted of about 150 mature basidia, each bearing four black spores. These basidia, collectively, therefore appeared to make up a single generation of approximately equal-aged members.

A few minutes after the black area just described had been focussed, it was noticed that at the periphery of the area some of the basidia were discharging their spores. Each basidium shot off its four spores in succession. Sometimes this process took less than five minutes, but sometimes longer. Since the gill had its natural orientation, the spores, on being discharged into the air, did not fall on to the hymenium again, but settled at the bottom of the dish. After a little while, spore-discharge became general

over the whole area. Most of the spores disappeared within half an hour, and the whole area was cleared in an hour and a half after the beginning of the observations.

In consequence of losing its spores, the black area became a white area. Whilst this change was going on, the surrounding white area had been turning into a dark area, owing to the fact that its spores, originally colourless, had begun to develop a brown pigment. Thus the original colour scheme became reversed: the black area surrounded by a white became converted into a white area surrounded by a black.

Now a little while before and also during the discharge of the spores from the first generation of basidia observed on the black area, a second generation of basidia could be distinguished rising into prominence. These new basidia occupied positions in the hymenium between the old ones and, in their totality, were similar to the old ones both in number and distribution. When the basidia of the first generation were discharging their spores, those of the second had already attained their full body-length and protruded to the maximum extent beyond the general level of the hymenium. Moreover, they were developing their sterigmata. For about forty-five minutes after the discharge of the spores of a first-generation basidium, it was also observed that no trace of spores could be perceived upon the sterigmata of the adjacent second-generation basidia, but at the end of this time the spores began to develop. About one hour and ten minutes after the discharge of the old spores, the new ones were about half-grown and, in the course of about another twenty minutes, they became full-grown. After attaining full size, the new spores remained colourless for some time—in one carefully observed instance for about an hour and a half. They then began to turn brown, and they became black in about an hour and a half. Perhaps the pigment still continued to accumulate for some time after this, although no further blackening could be observed. After the spores had turned black, they remained on the sterigmata for about three hours and a half and were then discharged.

If we date the second generation of basidia from the time of discharge of the spores of the first generation, we may say that

its course was run in about eight hours. To summarise for a single basidium, the time was occupied as follows :

(1) Finishing the development of the sterigmata after discharge of the spores on adjacent first-generation basidia, about . .	45 minutes
(2) Developing spores from their origin to full size	45 minutes
(3) Full-sized spores remaining colourless and receiving contents from the basidium .	90 minutes
(4) Full-sized spores turning brown and finally black	90 minutes
(5) The further maturing of the spores (and possibly the further accumulation of brown pigment), ended by violent spore-discharge, about	210 minutes
Total time . .	about 8 hours

We are now in a position to explain the rule of mottling already mentioned (p. 252), namely, that when a gill of *Panaeolus campanulatus* is observed with the naked eye the dark areas always exceed the light in extent. From the data obtained with the microscope and given above, we can divide the eight hours occupied by the hymenial area in the development of the second generation of spores into three subdivisions as follows :

(1) A white period of 3 hours, at the end of which the spores are of full size but still colourless.
(2) A brown or intermediate period of 1·5 hours, during which the spores turn brown and finally black, and
(3) A black period of 3·5 hours, during which the spores remain black, ending with spore-discharge.

Now to the naked eye, as soon as the spores begin to turn brown, they come to have a very dull appearance. On looking at the hymenium without the microscope, one therefore naturally divides the areas into light and dark, the dark including not only those

which have black spores but those which have brown. This being so, it follows from the observations recorded above that an unmagnified area, during the development of the second generation of spores observed, will appear light for about 3 hours and dark for about 5 hours. Since every other area has its light and dark periods divided in a similar manner, and since all the areas at one and the same time are in diverse stages of development, it is clear that to the naked eye, on the average, the surface extent of the dark areas will exceed that of the light areas in the proportion of about 5 to 3. The general correspondence of this calculation with the truth may be judged by the reader from an inspection of Fig. 88 (p. 252).

Successive Generations of Basidia.—As soon as the second observed generation of spores had been shed, a third began to develop. The basidia of the third generation arose and went through a series of developmental changes exactly similar to those already described for the basidia of the second generation. After the third generation of basidia had shed its spores, a fourth generation of basidia took its place, and so on. Altogether in the course of three complete diurnal periods, *i.e.* 72 hours, I observed seven successive generations of basidia upon the same area. The gradual development of the hymenium continued steadily through the nights as well as through the days, so that it appeared to be unaffected by light. It is perhaps almost needless to say that my eye was not continuously fixed on the area under study for the whole of the 72 hours : rather, observations were made at frequent intervals, every hour or so. During certain brief periods when I found it necessary to rest, S. G. Churchward kindly took my place at the microscope. At night the gill was only illuminated when it was necessary to observe it. The temperature of the laboratory was maintained at about 20° C.

As the fruit-body grew older, the rate of development of the hymenium diminished. The third generation of basidia completed its development more slowly than the second, the fourth more slowly than the third, and so on. The actual times between the spore-discharges were noted and are given in the following Table.

Rates of Development of Successive Generations of Basidia on a Gill of Panaeolus campanulatus.

Between the Discharge of the Spores of:	Approximate Time elapsing was:
The first generation observed and the previous generation	more than 3 hours
The first and second generations	about 8 hours
The second and third generations	about 9 hours
The third and fourth generations	about 10·3 hours
The fourth and fifth generations	about 11·3 hours
The fifth and sixth generations	about 15·3 hours
The sixth and seventh generations	somewhat more than 15 hours
Total time of observation	3 days and 3 nights

After the seventh generation of basidia had been produced, the hymenium was practically exhausted, and no further development took place. However, a few basidia were still left undeveloped. Perhaps under more favourable conditions of existence these might have given rise to yet another generation of spores.

The number of basidial generations actually observed as coming up in succession on the same small area of gill-surface was seven. The total number, including those unobserved, must have been more than this. The fruit-body was taken for observation when it had already been shedding spores for some 24 hours. Supposing that we reckon that the early unobserved generations took about as long to go through their cycle as the first one observed, *i.e.* about 8 hours, we must add at least two further generations to the seven actually observed. If, too, we suppose that the few basidia left at the end, under more favourable conditions of growth, would have produced one more final generation, we should have a total of ten generations altogether.

We may therefore conclude that any one small area of the hymenium of *Panaeolus campanulatus*, in the course of its development, produces about ten generations of basidia which come to maturity and shed their spores in succession.

When the original black area was first focussed, it possessed a peculiar contour of its own. The question may be asked: did

this area retain its individuality from first to last throughout its development ? One cannot answer with an unqualified yes. The fact is that, whilst the earlier generations of basidia were being produced, the contour of the area remained practically unchanged ; but, whilst the later generations were being produced, some parts of the area lagged considerably behind others in development. Into the details of the alteration of the individuality of the original area it is unnecessary to go. It will be sufficient to say that, in arriving at the estimate of the amount of time which was required for the maturation of each successive generation, my attention was fixed on one and the same small part of the area.

Another question arises in connection with the density of distribution of the spore-bearing basidia : was this density the same for all the generations ? The spaces separating the basidia of the first generation observed were equal to those shown in the central black area of Fig. 89 (p. 257). The number of basidia per square 0·1 mm. in the second, third, and fourth generations observed, was about the same as in the first generation. Then a diminution took place. The basidia of the fifth generation were, on the average, farther apart than those of the first, second, third, and fourth ; and those of the sixth and seventh farther apart than those of the fifth.

The significance of gill-mottling and the economy involved in the production of successive series of generations of basidia have yet to be discussed ; but it will be of advantage to postpone this discussion until the reader has first been made acquainted with the structure of the hymenium in detail. As we shall see, the task of interpreting the nature of the hymenial elements will be considerably facilitated by the knowledge, based on direct observation, that, on any small hymenial area, the basidia come to maturity in a series of successive generations.

Description of the Hymenium of Panaeolus campanulatus in Detail.—Previous descriptions of the hymenium of the Non-Coprinus Agaricineae have all been incomplete. Where mottling of the gills occurs, as in the Panaeoli and *Psalliota campestris*, the production of successive generations of basidia has been overlooked. There has usually been some doubt whether *paraphyses, i.e.* elements

destined from the first to remain sterile, are present in the hymenium or not. When it has been asserted that paraphyses are present, no sufficient means has been pointed out to distinguish them from the young basidia. So far, also, no account has ever been given of the changes which take place in the exhausted basidia ; and certain investigators even hold that, in some species, a basidium may produce more than one generation of spores.[1] Finally, no mycologist in recent decades has attempted to make a correct drawing of the hymenium as seen in surface view, so that, hitherto, the relations of the hymenial elements to one another in space have been nowhere sufficiently illustrated.[2]

One of the best illustrations of the hymenium of an Agaric hitherto published is that of *Russula rubra* in Strasburger's well-known *Text-book of Botany*.[3] In this, in cross-section only, are shown one cystidium, four spore-bearing basidia, and some eight other club-shaped elements. The largest of these sterile elements is labelled with a *p* which, according to the text, stands for paraphysis. There is nothing said to help the reader to interpret the nature of these cells. Are these eight elements destined to remain sterile, or are they of mixed nature, some being young basidia, *i.e.* about to produce spores, and others permanently sterile paraphyses ? The student is left to guess the answers to these questions. Then again, the illustration is unsatisfactory in that it does not contain any exhausted basidia, *i.e.* basidia which have shed their spores. It is unlikely that any student would take a gill for sectioning at the precise moment when it was about to shed its very first spores. Usually, in laboratory practice, a pileus is taken when it has been shedding spores for some time. In a typical hymenial illustration, therefore, some exhausted basidia ought to be included. From this discussion, I think it

[1] *Vide* Chap. I, p. 27.

[2] For surface-view illustrations of Non-Coprinus Agaricineae we have to go back to the pioneers in the investigation of the hymenium of the Hymenomycetes, *e.g.* Léveillé (1837), Berkeley (1838), Corda (1839), etc. Brefeld, in 1877, gave a plan of the relative positions of the basidia and paraphyses for a species of Coprinus (*Untersuchungen*, Heft III, Taf. IV, Figs. 10 and 14).

[3] Strasburger, Schenck, Noll, and Karsten, *A Text-book of Botany*, Third English (based on eighth German) edition, London, 1908, p. 408.

must be admitted that, although the individual elements of the hymenium in Strasburger's illustration have been carefully drawn, yet the real difficulties in the interpretation of their nature have been slurred over. Sachs' illustration for *Psalliota campestris* will be dealt with when we come to a discussion of the hymenium of that species. A criticism of any other hymenial illustrations is unnecessary, as what has been said already in connection with Strasburger's is practically of general application. In what follows, the author hopes to lay before the reader a more complete account of the hymenium of a Hymenomycete than has ever before been given.

In investigating the hymenium of *Panaeolus campanulatus*, the work was begun with a realisation of two important deductions which are based on the already recorded discoveries made with the horizontal microscope. These deductions are as follows: (1) the arrangement of the hymenial elements must have some relation to the coming to maturity of successive generations of basidia, and (2) after the beginning of spore-discharge, the hymenium must become progressively fuller of exhausted basidia.

The first difficulty to be overcome was the finding of the exhausted basidia—elements which previous workers had either neglected or overlooked. A gill was therefore placed in a compressor cell, and the basidia on its upper surface, which were discharging spores, were watched with the microscope. The results of my observations were as follows. A basidium which has just shed the last of its four spores continues for some twenty minutes or half an hour to protrude somewhat above the general level of the hymenium and to display its four stiff, slightly divergent sterigmata (Fig. 93, A, *c*). At the end of this interval, however, it undergoes two changes, one of which concerns its body and the other its sterigmata. The body of the basidium, in the course of a few seconds, contracts in length, and at the same time its convex outer end sinks inwards towards the hymenium and becomes *concave* (Fig. 93, A, *d*, *e*, *f*, *g*; also Fig. 96, *x*, p. 287). Owing to this change, the sterigmata are dragged into the concavity which has arisen; they are also drawn nearer together, and their ends, which were originally somewhat divergent, become sharply convergent. If

such a basidium be now looked at in side view in a cross-section of the hymenium, it no longer appears turgid and well-defined, no longer protuberant, but shrunken both in length and breadth,

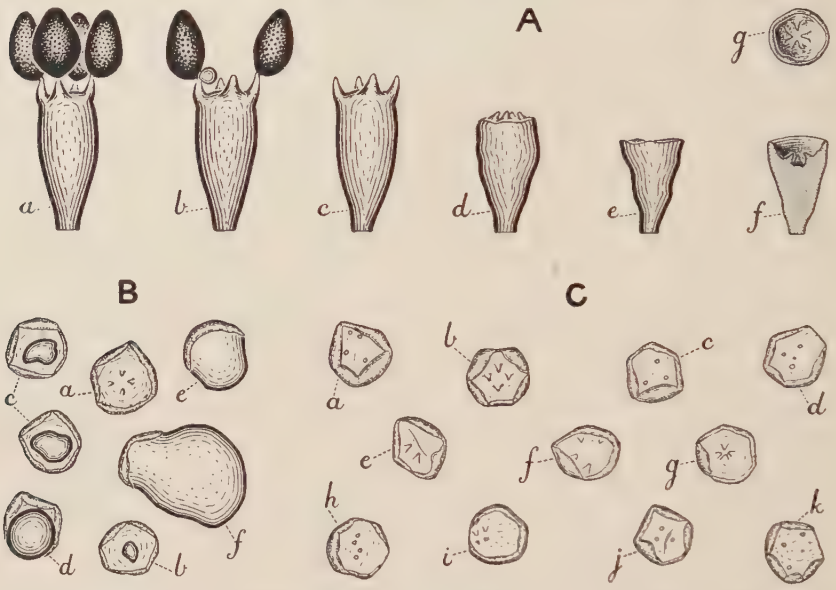


FIG. 93.—*Panaeolus campanulatus.* A, the collapse of exhausted basidia, seen in lateral view: *a*, a basidium with four ripe spores; *b*, a basidium which has shot away two spores and is about to shoot away another spore which has a full-size water-drop excreted at its hilum; *c*, a basidium which has just shot away its last spore but still has erect sterigmata; *d*, a basidium in the act of collapsing, about 20 minutes after the stage *c*, the sterigmata are sinking into a concavity forming at the end of the basidium-body; *e*, a completely collapsed basidium, the sterigmata in the concavity cannot be seen; *f* is *e* in vertical section, showing the sterigmata in the concavity; *g* is *f* seen from above. B, the tops of certain collapsed basidia which were in a gill mounted in water under a cover-glass. To show how air-bubbles are caught in the concave ends of the basidium-body: *a*, a basidium without an air-bubble; *b*, *c*, *d*, *e*, and *f* show bubbles of increasing size. C, the ends of collapsed basidia, as seen in a gill mounted with water below and air above: in *b*, *e*, *f*, *g*, and *i* the sterigmata are still distinctly conical, while in *a*, *c*, *d*, *h*, *j*, and *k* the sterigmata are reduced to mere refringent particles. Magnification, 700.

reduced to about one-third of its original volume, moulded more or less by the pressure of adjacent living basidia and paraphyses, and relatively difficult to observe (Fig. 93, A, *e*; also Fig. 96, *a*, *a*, p. 287). Its outer end no longer appears convex but *flat*, owing to the fact that one can only see the rim of the concave depression which has been formed in it. The sterigmata, in such a lateral view of the basidium, cannot be observed at all. This is due to the

fact that they are concealed within the concavity, which for optical reasons escapes observation. There can be no doubt that such an exhausted and shrunken basidium as has just been described is no longer living ; and we are justified in concluding that a *basidium dies within about twenty minutes to half an hour after shedding its last spore.*

The sterigmata, after being dragged downwards into the concavity at the end of the shrunken basidium, become more or less melted down into mere stumps (Fig. 93, C, *a*, *c*, *d*, *h*, *j*, *k* ; also Fig. 94, A and B, p. 276). Their remains continue to persist as small lumps of refringent matter, which do not disappear until the hymenium is utterly exhausted and begins to undergo putrefaction.

If a gill which has been discharging spores is placed flat on a glass slide and covered with a cover-glass, and if water is then allowed to run between the cover-glass and the upper hymenium, it may be observed that the water, as it progresses over the hymenium, often leaves behind a tiny bubble of air over the top of each exhausted basidium (Fig. 93, B). The same effect can be obtained with glycerine or chlor-zinc iodine. The bubbles are caught in the concavity at the end of each basidium-body. Such bubbles may help one in distinguishing exhausted basidia in both surface and cross-sectional views of the hymenium.

A study of exhausted basidia was made upon the gill of a fruit-body of *Panaeolus campanulatus* obtained in the wild state from a field, and the accompanying drawing (Fig. 93, C) shows the appearance of a number of these elements. In each case the rim of the concavity at the end of the exhausted basidium can be clearly seen, and from its somewhat irregular shape the conclusion may be drawn that the concavity is not very symmetrical. It was necessary to focus downwards from the rim in order to see the bottom of the concavity and so perceive the four sterigmatic stumps. The latter are aggregated in various ways in different basidia, doubtless on account of irregularity in the disposition of the walls of the different concavities.

An exact knowledge of the nature of exhausted basidia is of great importance for our investigation of the structure of the hymenium, for it enables us to tell with certainty whether a hymenial

element seen from above is or is not an exhausted basidium. A basidium which has shed its spores on the first day of spore-discharge is perfectly recognisable as an exhausted basidium on the last day of spore-discharge, *i.e.* after an interval varying from about a week to eleven days ; for, even then, it still retains its concave end in which may be seen more or less distinctly the four sterigmatic stumps. We are thus provided with a clue which enables us to distinguish past-generation basidia from present-generation basidia which are bearing spores, and from future-generation basidia which are as yet spore-less.

In studying the arrangement of the hymenial elements, it is best to begin with a surface view and to use only living material. Fixing, staining, and sectioning with the microtome, the method which has proved so valuable for research in plant histology generally, is here of little or no use owing to the fact that, when a hymenium has been killed, the basidia and paraphyses lose their turgidity and, therefore, do not stand out so sharply as when they are living. Moreover, in a microtome section, one finds that most, if not all, of the older spores, *i.e.* those which are in a state of development a little prior to their discharge, have been separated from their sterigmata. In making a preparation, it is best to take a gill straight from a fruit-body growing under as natural conditions as possible. For my investigations, gills were removed, as required, from fruit-bodies of *Panaeolus campanulatus* growing on horse dung in the laboratory. When a gill had been procured, it was placed flat on a glass slide and covered with a cover-glass. A drop of water was then placed at the edge of the cover-glass, under which it was sucked by capillary attraction. As it passed slowly over the upper hymenial layer, in several places it left the spores standing undisturbed on their sterigmata and did not drag them all off as it usually does under similar circumstances in Coprini and some other Agaricineae. By mounting a living gill in the manner just described, it became possible for me to observe all the basidial elements as they are in nature. It was sought not merely to get a general impression of the arrangement of the elements on different areas of the hymenium but, more especially, to find the exact arrangement of the elements on one particular area. Therefore my attention became concentrated on

an area measuring only one two-hundredth part of a square millimetre. It is to be remarked that the gill, before being removed from the fruit-body, had been shedding spores for about 24 hours, so that it was quite certain that it contained a considerable number of exhausted basidia. The results of the analysis of the area under study will now be given in detail.

The area investigated was part of what we have called, in discussing the phenomenon of mottling, a *black* area, *i.e.* it contained several almost equal-aged basidia all bearing black spores. These basidia, which were six in number, belong to what we shall henceforth call the *present generation*. They are shown in their proper positions relatively to the other hymenial elements in Fig. 94 at A. It will be noticed by reference to this Figure that the bodies of these basidia have the maximum diameter and that no two of them are in contact with each other. Basidia of any one generation are always separated by other elements. If they were not, it is easy to see that at maturity, owing to the fact that the perimeter which would include the four spores is always greater than the perimeter of the basidium-body, the spores of any two adjacent basidia would seriously interfere with each other and prevent free development and discharge. The avoidance of this mutual interference by means of suitable spacing is one of the most beautiful points in the organisation of the hymenium. It can be realised best by the study of a large area such as that shown in Fig. 89 (p. 257). The present-generation basidia in the small area under discussion have been set out by themselves in Fig. 94 at C.

We may now turn our attention to the *past generations* of basidia, *i.e.* to those generations which have already shed their spores and the members of which are now in the collapsed condition. These exhausted basidia can be distinguished by their size, somewhat irregular outline, sterigmatic stumps, and by the absence of protoplasmic contents (Fig. 94, A, *a*). They are also non-protuberant: if one has just focussed the tops of the bodies of basidia of the present generation, then one has to focus downwards in order to bring the tops of the exhausted basidia into view. The basidia of the past generations all look approximately alike: one cannot distinguish one past generation from another. In Fig. 94 at B all

the basidia belonging to the past generations have been set out by themselves. There are twelve of them altogether, if those shown

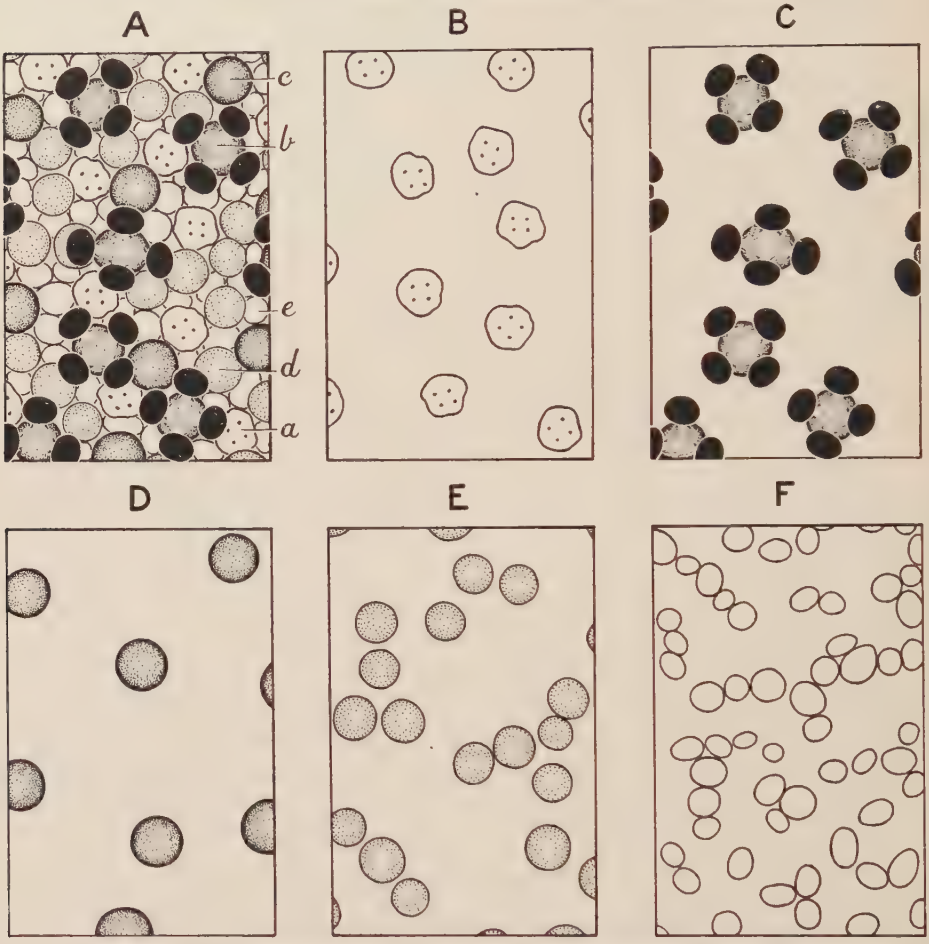


Fig. 94.—*Panaeolus campanulatus.* Analysis of the hymenium as seen in surface view on the second day of spore-discharge. A, an area equal approximately to 0·005 square mm. (0·06 × 0·09 mm.). This area contains: (1) *past-generation basidia, a,* which are recognisable by their four sterigmatic stumps and which are set out separately at B; (2) *present-generation basidia, b,* each of which bears four black spores and which are set out separately at C; (3) *coming-generation basidia, c,* heavily shaded with dots and set out separately at D; (4) *future-generation basidia, d,* smaller than the coming-generation basidia and slightly shaded with dots, set out separately at E; and (5) *paraphyses, e,* not shaded and partly hidden by the other elements, set out separately at F. Magnification, 580.

in part be included in the count. This number is twice that of the present-generation basidia present on the same area. The inference

is clear: the number of past generations of basidia, which the collapsed basidia really represent, is two. So far then, in classifying our basidia, we have accounted for two past generations and the present generation. We must now seek out the generations which are coming or are still to come.

What we may term the *coming generation* of basidia, *i.e.* those basidia which will rapidly come to maturity and produce spores immediately after the present generation of basidia has become exhausted, can readily be made out. They are distinguished individually from other young basidia by the fact that, unlike these, they have attained their maximum diameter and have already become protuberant. Eight of them are present in the area under discussion and, in order to help the reader in finding them in Fig. 94, A, they have been set out by themselves in Fig. 94, D. The diameter of their bodies is equal to that of the bodies of the basidia of the present generation. The only protuberant elements in the hymenium are the basidia of the present and the coming generations. In our area, the basidia of the coming generation have already reached their maximum protuberancy, *i.e.* their bodies project above the general surface of the hymenium just as far as those of the basidia of the present generation. The basidia of the coming generation are also densely filled with protoplasm which, so to speak, is waiting to be put into the spores when these have been produced. On the other hand, the basidia of the present generation are poor in protoplasm owing to the fact that the transference of this substance to the reproductive bodies has already been partially or completely accomplished. The basidia which are younger than those of the present generation, like the latter, are full of protoplasm, but their contents, owing to smaller volume, are much less conspicuous to the eye. In some areas similar to the present one, it was found that, shortly before the spores of the present generation of basidia are to be discharged, the sterigmata of the basidia of the coming generation are in course of development. In the area taken for our analysis, however, the sterigmata were not observed. Probably the time had not yet come for their development. It may be said that, when an area of the hymenium has begun to shed spores, two generations of basidia are undergoing development

simultaneously, the present and the coming. The latter, however, is some eight or nine hours less advanced than the former. When a basidium of the present generation is developing its spores, a basidium of the coming generation is elongating so as to become protuberant, and filling with protoplasm. When the former is getting ready to shed its spores, the latter is developing its sterigmata. Again, when the former is collapsing after shedding its spores, the latter is beginning to develop its spores.

We must now turn our attention to what we may call the *future generations*, *i.e.* to generations of basidia which will be developed in succession after the coming generation has reached maturity. These later generations are represented by basidia which relatively are much smaller and less conspicuous than those of the coming generation. Eighteen of these elements are to be found in the area we are studying, and they are shown in Fig. 94, A, at *d*. They have also been set out by themselves at E. Their smaller size, non-protuberancy, and relatively less conspicuous contents enable one to distinguish them from the basidia of the coming generation ; but one cannot with certainty distinguish one future generation from another. The basidia of the future generations are distinguished from those of the present generation by the absence of spores, and from those of past generations by the absence of the sterigmatic stumps, by their more symmetrical outline, and by their fine protoplasmic contents. The only elements with which the basidia of the future generations can be confused are the *paraphyses*. However, as a rule, these latter elements, which we shall treat of in greater detail directly, are relatively smaller and, owing to their large vacuoles, contain relatively little protoplasm. In Fig. 94 at A, the basidia of future generations (*d*) are all shaded with dots, while the paraphyses (*e*, shown by themselves at F) are left altogether unshaded. There can be little doubt that the eighteen basidia which are younger than those of the coming generation, represent several distinct generations. The number could not be less than three, if the same spacing as is seen for the basidia of the present generation is to be maintained. But, since we know from our observations with the horizontal microscope that the spacing of the basidia of future generations is not so compact as that of

earlier generations, we have a right to conclude that the eighteen basidia represent more than three generations. The number is probably about five.

The successive generations of basidia have been enumerated in their entirety. We must now turn our attention to those other elements of the hymenium which are called paraphyses. I have studied paraphyses in various Coprini, in Bolbitius, *Psathyrella disseminata*, *Lepiota cepaestipes*, *Stropharia semiglobata*, etc., and my conception of their nature may be stated as follows. Paraphyses are hymenial cells *sui generis*, which (1) numerically constitute a large proportion—often 50 per cent. or more—of the total number of hymenial elements, (2) usually differ more or less in shape from the cystidia and basidia, (3) as they grow older and larger, become progressively poorer in protoplasmic contents, and (4) never produce either sterigmata or spores, so that they remain sterile from their first origin to their death. I regard paraphyses as destined from their first origin to remain sterile. I see no reason to believe that, after spore-discharge has begun, any paraphysis ever turns into a basidium or, *vice versa*, that any young basidium ever turns into a paraphysis. The question now arises whether or not paraphyses occur in the hymenium of *Panaeolus campanulatus*.

If one cuts a transverse section through the hymenium of a gill that has been shedding spores only for a short time, say 24 hours, and if one studies the section with the microscope, it is not very easy to decide the question of the presence or absence of paraphyses. True it is that one can see here and there some small hymenial elements pushing up, as it were, between the bases of undoubted basidia and developing one or more vacuoles in their interior, but other cells which are similar in shape, not much larger, provided with but slightly more protoplasm, and which presumably are young basidia, occur along with them. One feels insecure when one pronounces that this small cell is a paraphysis but this other, differing from it so little in shape, size, and contents, is a very young basidium. The difficulties in distinguishing paraphyses from basidia are, however, not insurmountable, provided that they are approached in a suitable manner.

In devising a new method for solving the problem of the presence

or absence of paraphyses, I made use of the discovery already recorded that exhausted basidia can always be distinguished from other elements by their concave ends and by the sterigmatic particles which remain on their tops after collapse has taken place. It was argued that, if one were to study the surface of a hymenium in face view, from the beginning to the end of spore-discharge, then not only would the basidia become more and more easily recognisable owing to more and more of them becoming exhausted, but the paraphyses with their plain rounded tops should become, by contrast with the basidia, more and more conspicuous. It also seemed probable that the hymenium, after the spores had all been discharged, would present to the eye only two kinds of elements : (1) exhausted basidia to be distinguished by their sterigmatic particles, and (2) sterile paraphyses to be distinguished by their smooth rounded tops and impoverished protoplasmic contents. With a view to testing these suppositions, a fruit-body of *Panaeolus campanulatus* was grown on horse dung in the laboratory ; and from its pileus, day by day, from the beginning of spore-discharge to the end, there was dissected off a succession of gills for microscopic study. The hymenium on each gill was examined in face view. The results of the investigation, which was continued for upwards of a week, fully justified the suppositions which had been made.

A small piece (one two-hundredth part of a square mm.) of a completely exhausted hymenial layer is shown in Fig. 95 at A, In it there are two kinds of elements only—exhausted basidia and paraphyses. A waste spore, *i.e.* one which did not succeed in leaving the hymenium, is shown on the right. The paraphyses of Fig. 95, A, are set out by themselves in Fig. 95, B. A count (including elements sketched in part only) results in the finding that on the whole area the basidia are about equal in number to the paraphyses. Actually, the basidia are to the paraphyses in the proportion of 47 to 50. The tops of the basidia, which are by far their widest parts, pass down into an attenuated shaft, and they rest on the tops of the adjacent paraphyses. The latter are almost spherical elements and, since they are turgid, are doubtless still living. *At the end of the spore-discharge period*, therefore, *the basidia are all dead and the paraphyses are all living.* The paraphyses, as comparative

examinations proved, gradually enlarge during the exhaustion of the hymenium and, by the end of the spore-discharge period, they have attained their maximum size. This is made very evident by a comparison of Fig. 94, F (p. 276), which shows the size of the paraphyses in a hymenium which has not long been shedding spores, and Fig. 95, B, which shows the size of the paraphyses in an exhausted hymenium. When the paraphyses have attained their

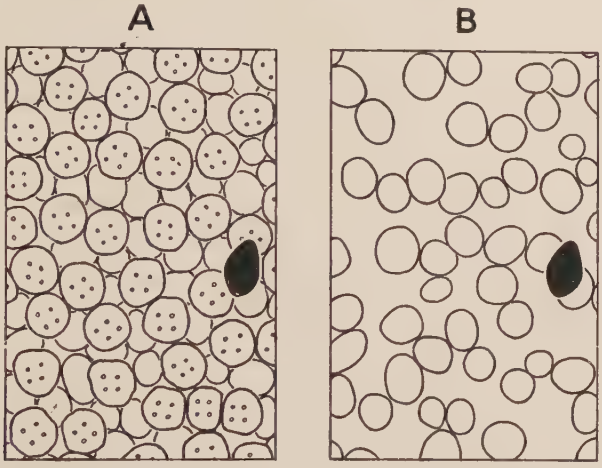


FIG. 95.—*Panaeolus campanulatus*. Analysis of the exhausted hymenium from a fruit-body which has ceased to shed spores. A, the basidia (all belonging to past generations) can be recognised by their sterigmatic stumps: they slightly overlie the paraphyses. One waste spore lies on the hymenium. B, the paraphyses of A sketched by themselves. Magnification, 580.

full development, the layer of protoplasm upon their walls is very thin, and the major part of their contents consists of a large vacuole. In this condition, therefore, they are very transparent. Sometimes, in parts of an exhausted hymenium, aborted basidia are to be found. These can be distinguished from the paraphyses by their shape, which is more or less like that of a club, and by their protoplasmic content. The latter, although containing a large vacuole in its centre, still forms a thick layer round the wall, and it has a peculiar dense, granular consistence totally different from that of the thin lining layer in the paraphyses.

What is the function of the paraphyses ? In some Hymenomycetes, like the Coprini, *Lepiota cepaestipes*, and *Psathyrella disseminata*, in which the organisation of the hymenium (to be discussed later) differs from that of the Panaeolus Sub-type, the paraphyses are absolutely necessary to keep the spore-bearing basidia apart. In these species the paraphyses, which are of large size, are not merely in contact with one another but adhere together so as to form a continuous and firm tissue through the gaps of which the basidia protrude themselves at intervals. No doubt, under these conditions, the paraphyses, in addition to fulfilling their chief function of separating the basidia and therefore of preventing their mutual interference, also serve to support the basidia so as to preserve them in their upright positions. Further, they probably help to supply the basidia with water which is required to compensate for losses sustained in transpiration from the spores, etc. In *Panaeolus campanulatus*, however, the paraphyses have no very definite order and are not closely adherent (Fig. 94, F, p. 276 ; Fig. 95, B, p. 281), so that one often finds two basidia in contact with one another (Fig. 94, A ; Fig. 95, A). What, therefore, can be said for the function of the paraphyses in this species ?

Owing to the fact that the basidia in *Panaeolus campanulatus* come to maturity in a succession of generations, paraphyses are not necessary as space-making elements : any two spore-bearing basidia can be separated by immature or exhausted basidia. I do not think, therefore, that the paraphyses here have the same chief function as they have in the Coprini. On the other hand, the paraphyses are probably useful in supporting the spore-bearing basidia in upright positions, especially toward the end of spore-discharge when most of the basidia are dead ; and, doubtless, they also conduct water into the basidia which, when protuberant and bearing four spores, must often transpire considerable quantities of it. If there were no paraphyses in the hymenium, many or most of the basidia would stand isolated on their narrow bases, and they would all expose a much larger superficial wall-area. Surely, under these conditions, the basidia would have greater difficulty in taking up positions perpendicular to the gill-surface and also in obtaining the increased amount of water which would be required for

transpiration. The paraphyses, in respect to their increase in circumference in a direction parallel to the surface of the hymenium, bring an *element of elasticity* into the hymenium. For the basidia, the order of development and exact final thickness are fixed rather rigidly. The paraphyses, on the other hand, although at first all very small elements, come to have a relatively wide range of size toward the close of the hymenial activity. The difference in amount of variation in size between paraphyses and basidia will be realised by comparing in Fig. 95 (p. 281), the basidia in A with the paraphyses in B. Right up to the time of the coming to maturity of the first generation of basidia and often for some time after, the gills of *Panaeolus campanulatus* are expanding in superficial area. The paraphyses, during this expansion, themselves expand and thereby prevent the coming into existence of spaces between themselves, and between themselves and the basidia. Thus the hymenium is preserved as a continuous membrane and the basidia are kept in lateral contact with elements which live longer than they do and which, in respect to mechanical support and supply of moisture, can care for them during the whole of their existence.

Our surface-view studies have taught us the essential facts concerning the arrangement of the elements of the hymenium in space and time. We are now in a position to interpret the basidia and paraphyses when seen from their sides. A cross-section through a gill that has been shedding spores for some time, say 24 hours, is represented in Fig. 96. This illustration may be considered to be an enlarged portion of the lower third of one of the long gills of Fig. 85 (p. 249). However, it does not show the exact position of the elements as they were actually observed in any one particular preparation, but rather the generalised result of the study of a great many preparations, *i.e.* it is semi-diagrammatic : various details drawn originally with the help of the *camera lucida* have been brought together and combined by the author so as to construct synthetically an ideal section which embodies as many facts of normal structure as possible.

In Fig. 96, we can distinguish : the hymenium, *hy*, composed of a single layer of cells which are arranged perpendicularly to the plane of the gill-surface ; the subhymenium, *sub*, composed of two

or three layers of cells which are oval or rounded in shape and somewhat irregularly disposed ; and the relatively broad trama, *tr*, the elements of which are more or less cylindrical in form, in general elongated in a direction perpendicular to the pileus-flesh and parallel to the hymenial layers, and often anastomosing with one another.

On the left-hand side of the Figure, the section is represented as passing through : a white area of the hymenium, A ; a black area, B ; a brown area, C ; and another white area, D ; and on the right-hand side as passing through a black area, E ; a white area, F ; a brown area, G ; and another black area, H. These black, brown, and white areas correspond to similarly coloured areas which have already been described in surface view and which are shown in Figs. 89 and 90 (pp. 257 and 258).

It was pointed out that a study of adjacent areas of the hymenium of a gill of *Panaeolus campanulatus*, seen in surface view, leads to the conclusion that the hymenium is so organised that its development takes place in a series of waves of small dimensions which move irregularly and simultaneously through it [1] ; and by means of *camera-lucida* drawings, reproduced in Figs. 89 and 90 (pp. 257 and 258), the direction of the waves on two small areas was clearly shown. Now in transverse sections through the hymenium the wave mode of hymenial development can also be made out. It has therefore been indicated in Fig. 96 by means of an appropriate arrangement of the elements.

A wave of development in the hymenium on the left-hand side of Fig. 96 is represented as passing from above downwards. The basidia opposite the Roman numerals, I, II, III . . . XII developed their spores in succession. The basidia I and II shed their spores an hour or two ago and have collapsed. The basidium III shed its spores about 15 minutes ago and is in the act of collapsing : the sterigmata are being drawn into the concavity which is forming at the end of the basidium-body. The basidium IV is discharging its spores : two of them have already been shot away, and the lower one of the remaining two should be shot away at the end of about one second, for the drop of fluid excreted at its hilum has just attained its full normal size and is about

[1] *Vide supra*, pp. 258–259.

9 seconds old.[1] The basidia V, VI, VII . . . XII will all discharge their spores in succession, V first and XII last. The basidia opposite the Arabic numerals 1, 2, 3 . . . 11 have developed spores in the area A and will develop spores in the remaining areas, in their numerical order. It will be noticed that the basidia 1, 2, and 3 bear spores of progressively smaller size. Basidium 4 possesses full-grown sterigmata but no spores. The sterigmata on basidia 4, 5, and 6 are progressively shorter. Basidium 7, although fully protuberant, has not yet developed even the bases of its sterigmata, and basidia 8, 9, 10, and 11 are in the same condition. They will all develop their sterigmata in succession following their numerical order. The series of basidia 1, 2, 3 . . . 11 are developmentally about eight hours behind the adjacent series of basidia I, II, III . . . XII. Thus basidium 1 is about eight hours behind basidium I, basidium 5 about eight hours behind basidium V, basidium 10 about eight hours behind basidium XII, and so forth.

Another wave of development in the hymenium is shown on the right-hand side of Fig. 96 as passing from below upwards. There is a series of basidia indicated by the Roman numerals I, II, III . . . XI, where I is the oldest, II slightly younger, III still younger, and so on up to XI. Similarly, in the series of basidia indicated by the Arabic numerals 1, 2, 3 . . . 12, basidium 1 is the oldest, basidium 2 slightly younger, basidium 3 still younger, and so on up to basidium 12. Here again, the series 1, 2, 3 . . . 12 is developmentally about eight hours behind the series I, II, III . . . XI.

The developmental waves shown in the hymenium on both sides of Fig. 96 correspond in their nature to the wave *ac* to *b* shown in the surface view represented in Fig. 90 (p. 258), for they are continuous in one direction. In the surface view represented in Fig. 89 (p. 257), a wave is shown which has originated at the periphery of the area and is spreading centripetally, *i.e.* toward the centre of the central black area. If one wanted to represent a cross-section through a wave area of this type, one could

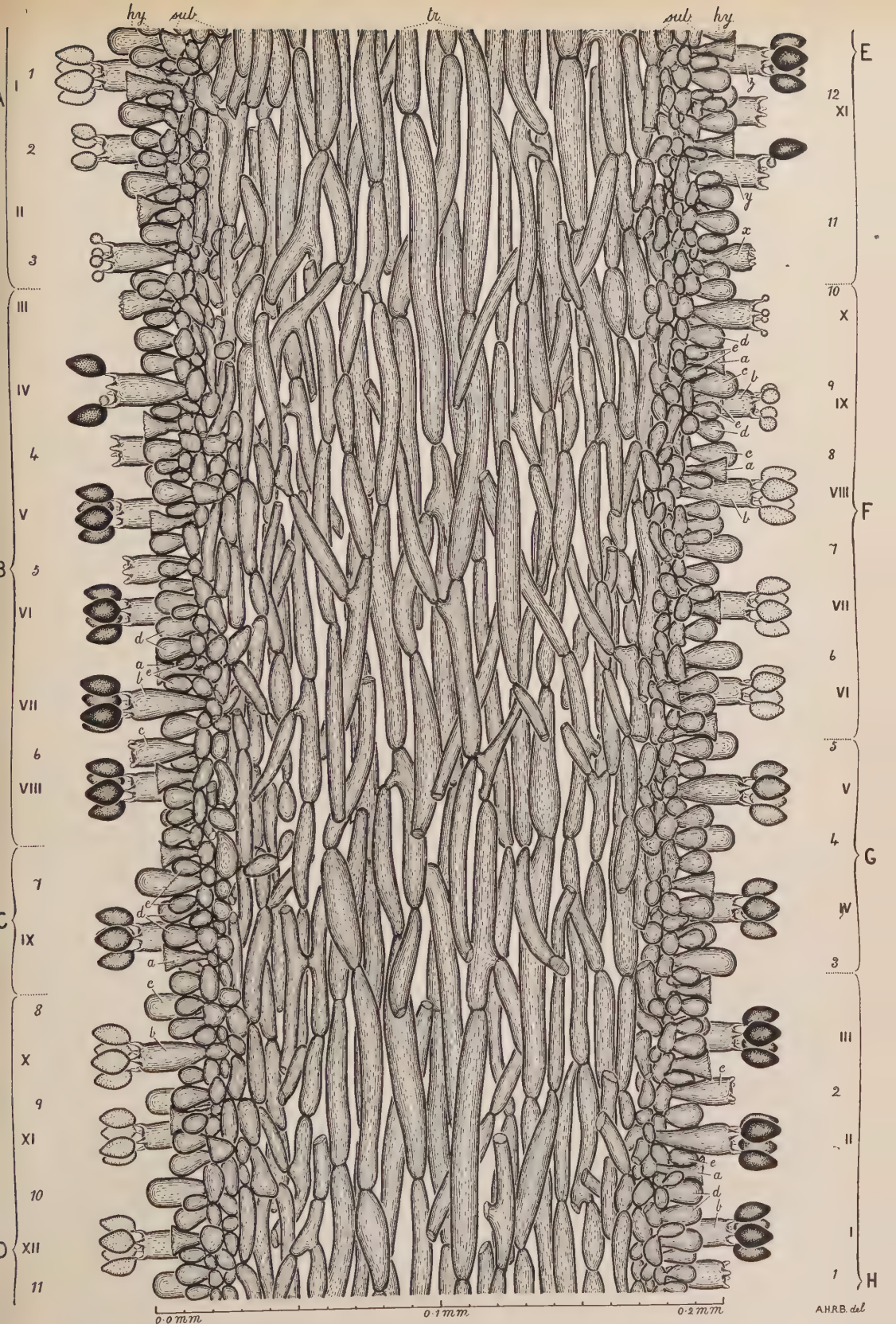
[1] The spores, normally, are shot away about 10 seconds after the water-drop begins to be excreted and immediately after it has attained full normal size. *Vide* Chap. I.

FIG. 96.—*Panaeolus campanulatus.* Semi-diagrammatic vertical section through part of a gill, 0·45 mm. long, showing the arrangements of the elements of the hymenium, subhymenium, and trama. On the left-hand side of the Figure, the section is represented as passing through: a white area of the hymenium, A; a black area, B; a brown area, C; and another white area, D; and, on the right-hand side, as passing through a black area, E; a white area, F; a brown area, G; and another black area, H. In the white areas, basidia of the present generation are very young, their spores being between 0 and 2·25 hours old and still colourless. In the brown areas, the basidia of the present generation are older, being between 2·25 and 3·75 hours old; their spores, which are brownish, are in the process of turning black. In the black areas, the basidia of the present generation are the most mature of all, their spores, which have already turned black, being between 3·75 and 7·25 hours old. The elements of the hymenium can everywhere be separated into the following five classes: (1) basidia of the *past generations*, *a*, which have discharged their spores and have collapsed; their ends are concave but look flat in the side view here shown; (2) basidia of the *present generation*, *b*, which are easily recognised because they bear spores; (3) basidia of the *coming generation*, *c*, which are protuberant; they may or may not have yet developed sterigmata (*vide* in B, C, and D, the basidia opposite the numbers 4, 5, 6, 7, 8, 9, 10, and 11) but have not yet developed spores; (4) basidia of *future generations*, *d*; these are non-protuberant and more or less pear-shaped; they will bear spores later on; and (5) the *paraphyses*, *e*, sterile elements which never bear sterigmata and spores; at this stage of the development of the hymenium, they are distinguished from the basidia of future generations by their smaller size, their position between the basidia, their contents, and their tendency to become more or less spherical as they enlarge.

A wave of development in the hymenium on the left of the Figure is represented as passing from above downwards. The basidia opposite the numbers I, II, III . . . XII, developed their spores in succession. The basidia, I and II, have shed their spores an hour or two ago, and have collapsed. The basidium III has shed its spores about 15 minutes ago and is in the act of collapsing. The basidium IV is about to shed its last two spores; one, which should be shot away the next second, has a drop of water of full size and about 9 seconds old attached to its hilum. The basidia V, VI, VII . . . XII will all shed their spores in succession. The basidia 1, 2, 3 . . . 11 will develop spores in succession in their numerical order. They are about 8 hours developmentally behind the adjacent basidia I, II, III . . . XII. Thus 1 is eight hours behind I, 5 eight hours behind V, 10 eight hours behind XII, etc.

Another wave of development is shown as passing upwards through the hymenium on the right-hand side of the Figure. Thus there is a set of basidia I, II, III . . . XI where I is the oldest, II the next oldest, and so on down to XI. Similarly in the series 1, 2, 3 . . . 12, 1 is the oldest, 2 the next oldest, and so on down to 12. Here again the series 1, 2, 3 . . . 12 is developmentally about 8 hours behind the series I, II, III . . . XII.

The exact size of every element may be read by using the scale at the base of the Figure. Magnification, 465.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accomplish it in Fig. 96 by removing the piece of hymenium on the left of the Figure from B VIII to the bottom of D, and by replacing it with the mirror-image of the remaining part of the hymenium which stretches from B 6 upwards. To observe such a mirror-image, it would only be necessary to place a mirror transversely across the Figure with its base along the line B 6 to G 5 and facing toward the top of the page. If a similar mirror-image were added to the upper half of the hymenium on the right-hand side of the Figure, we should have an arrangement showing a wave spreading centrifugally, *i.e.* outwards from the centre, like a wave started in the smooth water of a pond by a falling rain-drop.

The elements of the hymenium in the section represented in Fig. 96, can be separated everywhere into the same five classes which we differentiated from one another in our surface-view studies : (1) basidia of *past generations*, *a a*, which have discharged their spores ; their ends are concave but look flat in the side view here shown ; they are no longer protuberant ; (2) basidia of the *present generation*, *b b*, which are easily recognised because they are protuberant and bear spores ; (3) basidia of the *coming generation*, *c c*, which are protuberant but do not bear spores ; they may or may not have developed sterigmata as yet (*vide*, in the areas B, C, and D the series of basidia opposite the Arabic numerals 4, 5, 6 . . . 11 ; and on the opposite side of the Figure, in the areas, H. G, F, and E, the basidia of the series 1, 2, 3 . . . 11, as well as the basidium XI) ; (4) basidia of *future generations*, *d d* ; these are non-protuberant and more or less pear-shaped ; they will elongate and bear sterigmata and spores later on ; and (5) the *paraphyses*, *e e*, sterile elements which never bear sterigmata and spores ; at this stage of the development of the hymenium, they are distinguished from the basidia of future generations by their smaller size, their position between the lower parts of the basidia, their vacuolated contents, and their tendency to become more or less spherical as they enlarge.

The most prominent elements of the hymenium in a cross-section are the basidia of the present generation, for they alone bear spores. It will be of interest here to state the relative ages of these basidia as they are represented in the various areas of

Fig. 96. Such a statement is made possible through the application of the knowledge which was gained with the horizontal microscope in respect to spore-development. In the white areas A, D, and F, the basidia are relatively young, for their spores are only between 0·0 and 2·25 hours old. Some of these spores, A 2, A 3, F IX, and F X, which are only partially grown and therefore not yet of full size, are even less than an hour old. The others which have attained full size, A 1, D X, D XI, D XII, F VI, F VII, and F VIII, are still colourless: they are only partially filled with the protoplasm and reserve foodstuffs which are slowly passing into them from the basidium-bodies through the narrow sterigmatic passages. In the brown areas, C and G, the basidia of the present generation, C IX, G IV, and G V, are relatively more advanced, for their spores are between 2·25 and 3·75 hours old. These spores have received most of their contents from the basidium-body, and their walls have already become brown. The process of pigmentation, which will eventually turn the spores black, is in full swing, and the spore-walls are slowly deepening in tint. In the black areas, B, E, and H, the basidia of the present generation, B IV, B V, B VI, B VII, B VIII, E *y*, E *z*, H I, H II, and H III, are the most advanced of all; for their spores are quite black, between 3·75 and 7·25 hours old, and preparing themselves for the moment of discharge. Two of the basidia, B IV and E *y*, are in the very act of discharging their spores and have therefore attained the maximum age. From E *y* the last spore, and from B IV the last spore but one, should be shot away within about one second, for drops of fluid of full normal size have just been excreted from their respective hila.

The sporabolas of a number of spores, which have been shot from the hymenium and have fallen in still air, are shown magnified 20 times in Fig. 85 (p. 249). In Fig. 96 (p. 287), where the magnification is 465, it was found impracticable to represent any spore-trajectories owing to want of space on the page. A portion of Fig. 96 has therefore been reproduced in Fig. 97, and to it the sporabolic paths of several spores have been added. As in other Agaricineae, the four spores of each basidium of *Panaeolus campanulatus* are shot in succession outwards into an interlamellar

space. Each spore is projected more or less horizontally from its sterigma with a considerable velocity; but this horizontal velocity, in a small fraction of one second, is reduced to zero owing to the resistance offered to the passage of the spore by the air.[1] Each spore, after having been shot more or less horizontally to a maximum distance of 0·1–0·12 mm., makes a sharp turn through a right angle and then, if the air is still, falls

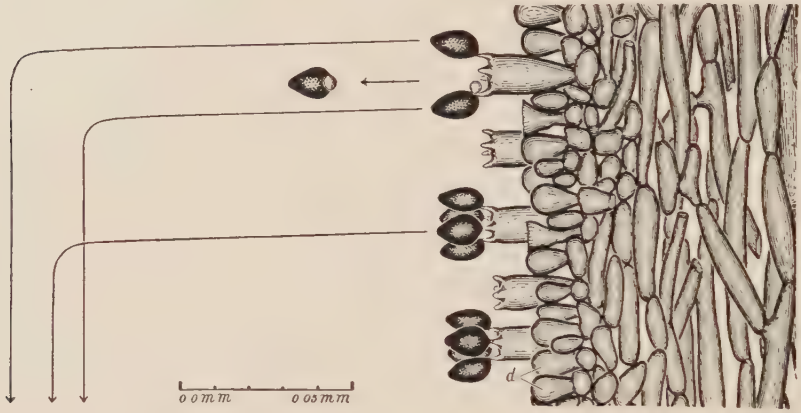


Fig. 97.—*Panaeolus campanulatus.* A vertical section taken transversely to the long axis of a gill showing the probable trajectories of spores discharged from the hymenium (a portion of the area B in Fig. 96, p. 287). The uppermost basidium has just discharged one of its spores which is being projected horizontally and is carrying a drop of water with it. From the hilum of another spore on the same basidium a water-drop has been excreted to about maximum size: this spore is just about to be discharged. Three trajectories of spores, discharged in still air, are indicated by the arrows; their horizontal portions have been represented as being (from above downwards) 0·12 mm., 0·1 mm., and 0·11 mm. in length. Magnification, 465.

vertically downwards toward the earth (Fig. 97). The steady terminal velocity of fall for a spore of *Panaeolus campanulatus* is about 2–3 mm. per second.[2]

In *Panaeolus campanulatus*, just as in all other Hymenomycetes, the drop excreted at the spore-hilum just before spore-discharge is carried with the spore during its flight through the air.[3] This is represented in Fig. 97 for the spore which has just left the uppermost present-generation basidium.

We have seen that all the elements represented in the

[1] Vol. i, 1909, p. 185. [2] *Cf.* p. 249, foot-note. [3] Chap. I, pp. 14–16.

hymenium of Fig. 96 belong to five classes. In order to demonstrate this point still more clearly, a small portion of the hymenium, namely, the black area B, has been represented in Fig. 98 on a larger scale and analysed in detail. This analysis of a piece of the hymenium in cross-section corresponds to the analysis given in Fig. 94 (p. 276) for a piece of the hymenium as seen in surface view.

In Fig. 98, at A, the elements represented are exactly similar to those shown in Fig. 96 (p. 287) in the area B, except for the fact that the subhymenium, *s*, has been toned down, so that by contrast the hymenium, *h*, stands out more clearly. At B, the four basidia of the past generations present in A are shown by themselves in their original relative positions. In a similar manner are represented: at C the basidia of the present generation, at D the basidia of the coming generation, at E the basidia of future generations, and at F the sterile paraphyses. No single hymenial element shown at A has been omitted in this analysis, but every one has been placed in one or other of the five classes represented in B, C, D, E, and F. The letters A, B, C, D, E, and F in Fig. 98 correspond respectively to the letters A, B, C, D, E, and F in Fig. 94 (p. 276). Just as the area B in Fig. 96 has been analysed in Fig. 98, so might be analysed any of the other areas of Fig. 96. There is no hymenial element represented in Fig. 96 which does not belong to one of the five typical classes; and an analysis of the hymenial elements of its areas B, C, F, and H, has been partially carried out by means of the letters *a*, *b*, *c*, *d*, and *e* which indicate past, present, coming, and future generations of basidia and paraphyses respectively.

So far we have dealt with a cross-section of a hymenium taken when the process of spore-discharge has been going on for only 24 hours; but the question may be asked: what is a cross-section of the hymenium like when several days have passed by and spore-discharge has ceased? The answer is given in Fig. 99. Here the trama, *t*, and the subhymenium, *s*, have been toned down so that the hymenium, *h*, may be more easily distinguished. At *w* are two waste spores which were not successfully discharged and are therefore clinging to the hymenial surface. The hymenium is

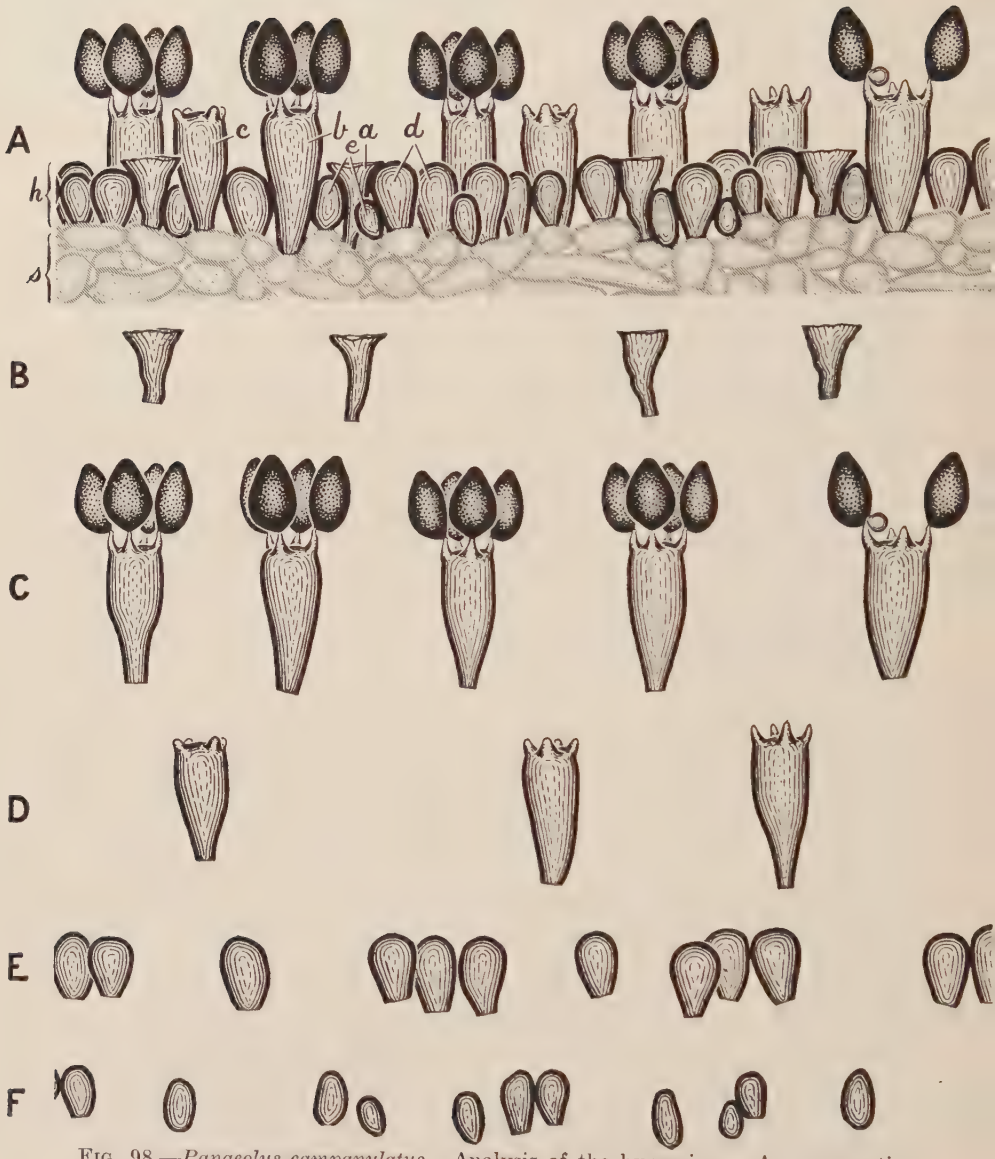


FIG. 98.—*Panaeolus campanulatus.* Analysis of the hymenium. A, cross-section through the hymenium *h* and the subhymenium *s* (same as area B in Fig. 96). The subhymenium has been softened so as to make the hymenium more distinct. The four past-generation basidia, *a*, are set out at B; the five present-generation basidia, *b*, are set out at C; the three coming-generation basidia, *c*, are set out at D; the twelve future-generation basidia, *d*, are set out at E; and the twelve paraphyses, *e*, are set out at F. The present-generation basidium farthest to right in A and C, has just discharged two of its spores and is about to discharge a third spore. That the moment of discharge for this third spore has arrived, is indicated by the drop of water, now of full size, which has been excreted within the last ten seconds from the spore hilum. Magnification, 718.

represented as being fully exhausted. Its elements are of two kinds only: exhausted basidia, *b*, and more or less globular paraphyses, *p*. The exhausted basidia can everywhere be distinguished by their shrunken bodies and flat ends. The paraphyses are everywhere rounded or oval in shape and appear to be fully turgid. By comparison with Fig. 98, A (p. 292), which represents the hymenium in an early stage of spore-discharge, it will be seen that the paraphyses are now much larger than they were. It is evident that, as more and more basidia shed their spores and collapse,

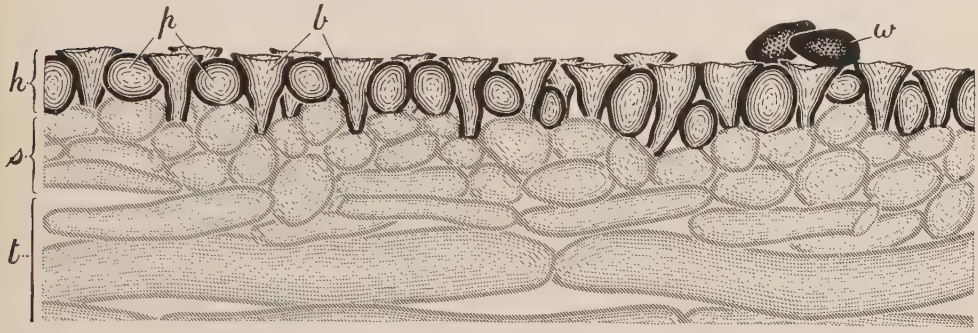


FIG. 99.—*Panaeolus campanulatus.* Cross-section through the hymenium, *h*, after spore-discharge has been completed. There are only two kinds of elements present: collapsed basidia, *b*, and swollen paraphyses, *p*. The tops of the basidia overlie the now rounded paraphyses. Two spores, *w*, which were not discharged, are shown lying on the hymenium. *s*, the subhymenium; *t*, the trama. The subhymenium and trama have been softened so as to make the hymenium more distinct. Magnification, 718.

the paraphyses gradually increase in size. This expansion on the part of the paraphyses makes up to a very considerable extent for the lateral shrinkage of the basidium-bodies. Owing to this compensation, the hymenium remains as a continuous membrane, even when it has become completely exhausted. Fig. 99, which shows the exhausted hymenium in cross-section, corresponds to Fig. 95, A (p. 281), which shows the exhausted hymenium in surface view.

Up to the present we have studied the hymenium in two of its stages of development only: (1) during the time that it is actively discharging its spores, and (2) after it has ceased to shed spores and has become completely exhausted. In order to complete our analysis, it is necessary for us to consider the state of the

hymenium before it has produced any spores at all. A description of the very young hymenium has been deferred until now because the author's investigations began with the older states of the hymenium, and because one can only understand the nature and arrangement of the elements of the very young hymenium in the light of the knowledge gained by a study of the older hymenium which is producing and discharging spores.

We shall consider the structure of the very young hymenium which has not yet produced any spores, in surface view first. A young gill was taken from a living fruit-body, placed flat on a slide, and covered with a cover-glass without the addition of any mounting fluid. The appearance of its hymenium is shown in Fig. 100 at A. One observes a large number of more or less prominent elements of various sizes projecting toward the eye. These elements are all basidia. The largest ones, indicated by the letter *a*, are the basidia of the first generation, *i.e.* those which will produce and liberate spores first. In the piece of hymenium under consideration, they had already attained their maximum diameter and their maximum protuberancy; while, in other areas of the hymenium on the same gill, some of them had already developed sterigmata or were in the act of doing so.

Several first-generation basidia can be seen scattered about over the area shown in Fig. 100, A. In this area can also be seen basidia of medium size, one of which is indicated by the letter *b*. These are the basidia of the second generation, *i.e.* basidia which will produce and liberate spores, after the basidia of the first generation, already referred to, have shed their spores and collapsed. The other basidia on the area, indicated by the letter *c*, are much smaller. They are evidently the basidia of the third, fourth, and subsequent generations, which will develop and liberate spores in the middle and last stages of the hymenial activity. The paraphyses are deeply seated and more or less hidden between the bases of the basidia, and no attempt has been made to indicate their positions in Fig. 100, A. In order to observe the paraphyses, a gill was mounted under a cover-glass in water, and the plane of focus of the microscope was lowered until the paraphyses were reached. In Fig. 100, B, the positions of some of the

overlying basidia are represented by dotted circles, while the paraphyses which were in part seen through the basidia are shaded with dots. It will be observed that the paraphyses are considerably

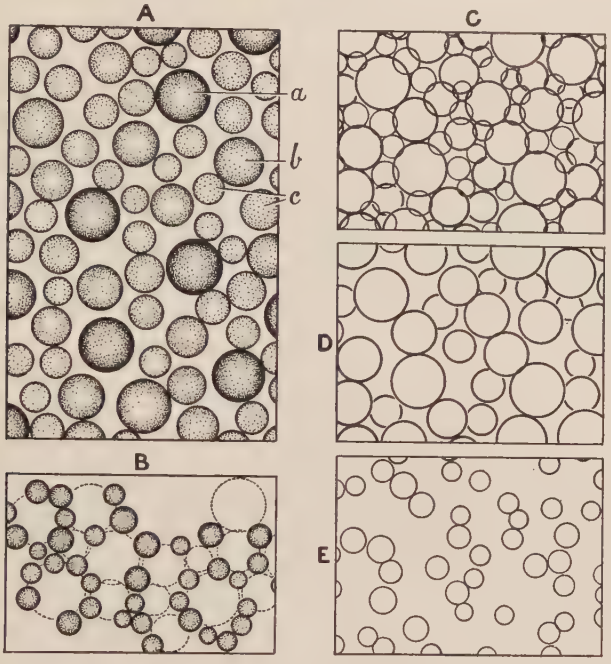


FIG. 100.—*Panaeolus campanulatus*. Analysis of a very young hymenium, seen in surface view, before any spores have been developed. A, (gill placed on slide under cover-glass, no water added) shows basidia only: those of the first generation, *a*, are the most prominent; those of the second generation, *b*, less prominent; and those of succeeding generations, *c*, least prominent. B, (gill mounted in water, plane of focus on the paraphyses) shows the paraphyses shaded with dots. The basidia, which are larger and overlie the paraphyses, have their positions indicated by broken circles. C, (gill mounted in water) a plan of all the elements in a small portion of the hymenium. The larger elements are the basidia which have been set out at D, and the smaller ones the paraphyses which have been set out at E. Magnification, 580.

smaller than the basidia, and are ensconced between the basidia, particularly where three basidia adjoin one another. Another portion of the hymenium, which was observed when immersed in water, is shown in Fig. 100, C. Here, every element of the

hymenium has been shown in outline. The larger elements are the basidia and the smaller ones the paraphyses. An analysis of this area is given at D and E. The basidia of C have all been represented at D, and, similarly, the paraphyses of C have all been represented at E.

If one compares the paraphyses in Fig. 100, E with those in Fig. 94, F (p. 276) and Fig. 95, B (p. 281), all of which have been drawn to the same scale, it is obvious that the paraphyses grow steadily in size during the gradual exhaustion of the hymenium. The paraphyses of an exhausted hymenium have diameters which are between two and three times as large as those of paraphyses in the hymenium just previously to the production of the first spores.

A transverse section through the very young hymenium, which has not yet produced any spores but is about to produce them, is shown in Fig. 101 in the upper drawing at *h*, while the subjacent subhymenium is shown at *s*. The more prominent and larger elements of the hymenium, *a*, *b*, *c*, are all basidia; while the smaller elements, *p*, ensconced between the lower parts of the basidia are all paraphyses. In order that the basidia and paraphyses may be the more readily distinguished from one another, in Fig. 101 a second (lower) drawing has been added. This is a copy of the upper drawing except for the fact that the subhymenium has been toned down and the paraphyses have been left unshaded. Of the basidia: the four prominent ones, *a a*, one of which has already developed sterigmata, are basidia of the first generation; the medium-sized ones, *b b*, are basidia of the second generation; whilst the smaller basidia, *c c*, are the basidia of the third, fourth, and all subsequent generations. The basidia *a b c* in Fig. 101 should be compared with the corresponding basidia *a b c* in Fig. 100, A (p. 295). The paraphyses of Fig. 101 also correspond with the paraphyses of Fig. 100, B.

We have now studied the hymenium of *Panaeolus campanulatus* in all those stages of its development which are subsequent to the coming into existence of its elements. We have seen that all its elements, before, during, and subsequently to spore-discharge by the fruit-body as a whole, are either basidia or paraphyses;

and we have been able to divide the basidia into those of past, present, coming, and future generations. Surface-view and cross-sectional illustrations have been given which are in harmony with one another, and which clearly indicate the relations of the hymenial elements in space and time. For the first time, the hymenium of a Non-Coprinus Agaric has been analysed in detail.

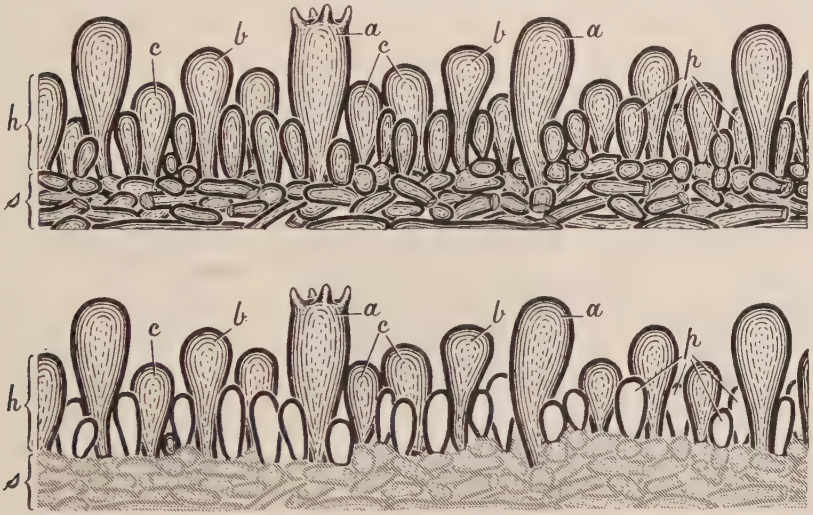


Fig. 101.—*Panaeolus campanulatus*. Above, a section through the very young hymenium, *h*, just prior to the development of spores by the first-generation basidia, and through the subhymenium, *s*. *a a*, basidia of the first generation; *b b*, basidia of the second generation; *c c*, basidia of subsequent generations; *p*, paraphyses. Below, a similar section but here the subhymenium has been softened so as to make the hymenium more distinct, and the paraphyses have been left unshaded so that their size, number, and arrangement relatively to the basidia become obvious at a glance. Magnification, 718.

The author feels that this marks a distinct stage in the advance of our knowledge of the wonderful way in which the fruit-bodies of the Hymenomycetes are organised for carrying out their one great function of producing and liberating spores.

Significance of the Development of the Basidia in Successive Generations on any One Hymenial Area, and of the Existence of Various Areas.—Now that we are acquainted with the arrangement of the elements in the hymenium in space and time, we are in a position to discuss the theoretical significance of the development of basidia in successive generations on any one hymenial

area and also the significance of the existence of the various areas to which the phenomenon of mottling is due.

In regard to the question of successive generations, it is first to be remarked that on any one area, owing to the fact that the basidia come to maturity in succession, a great many more spores are safely ripened and discharged than would be the case if the basidia were all to develop simultaneously. The space above any

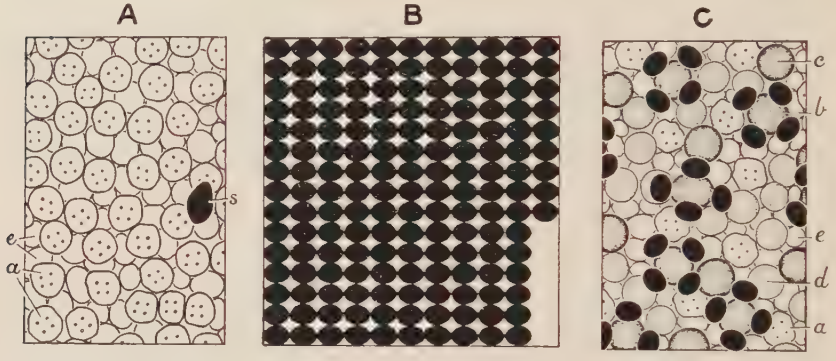


FIG. 102.—*Panaeolus campanulatus*. A, surface view of a piece of exhausted hymenium. The basidia had produced about 159 spores as shown by the number of sterigmatic stumps; *a*, exhausted basidia; *e*, paraphyses; *s*, a waste spore. B, the 159 spores of A set in the upright position close together; the area is about 1·5 times as large as A. C, a surface view of a piece of hymenium of the same size as A, seen in the middle of the spore-discharge period. The spores on A were distributed at any one time during the spore-discharge period as at C; *a*, past-generation basidia; *b*, present-generation basidia; *c*, coming-generation basidia; *d*, future-generation basidia; *e*, paraphyses. Magnification, 387.

given area for the protrusion of the basidia and the extension of their spreading sterigmata and spores is limited. If all the basidia on the area endeavoured to occupy it simultaneously, there would be nothing but confusion: the basidia would so jostle each other and interfere with each other's development that the spores would become matted together and their chance of successful ripening and discharge would be reduced almost to nothing. This can best be realised by reference to an actual area, one that was drawn with the *camera lucida* and is represented in Fig. 102, A. This area, as one may reckon by counting the number of sterigmatic stumps, produced 159 spores. Each spore in its upright position occupies a certain horizontal area. If all the 159 spores were to

be placed side by side in contact, as shown in Fig. 102 at B, they would occupy an area which is roughly one and a half times the original area. The impossibility of all the basidia on any area successfully producing and liberating their spores at one and the same time thus becomes obvious. The actual distribution of the spores on the area A at any one time during the spore-discharge period is indicated by the *camera-lucida* drawing reproduced in Fig. 102 at C. If all the spores produced on A were to be developed simultaneously and were to have the spacing shown at C, the area A would need to be made about seven times as large as it actually is.

It is clear from the above discussion that the production of successive generations of basidia enables a hymenium to produce and successfully discharge many more spores than would be possible if only one generation of spores were produced. Yet the further question remains : why should the succession on any small area take the form of successive generations of equal-aged or almost equal-aged basidia ? The answer may be obtained, perhaps, by comparing the basidia to soldiers. In order that a battalion shall pass across a narrow piece of ground, along a road, or through a pass, with the greatest speed and smoothness, it is organised into a column of fours. The soldiers in each four march shoulder to shoulder in step, and any one point on the line of march is passed by four after four at successive intervals. Efficiency in passing any given point in a given time by the whole force is only obtained by giving to each soldier suitable space-relations with his fellows in the same four and with those in the fours in front and behind. If a battalion becomes disorganised, so that each man loses his former space-relations with his fellows, it becomes reduced to a crowd of men who are apt to impede each other's progress by getting in each other's way. For the purpose of passing a given point on a road of limited width in a given time by a large number of men, the advantages of the column-of-fours arrangement over the go-as-you-please arrangement are sufficiently well known from experience. It seems to me probable, therefore, that the battalion method of bringing the basidia to maturity on any small area of the hymenium has come into existence in the course of evolution

because of its high efficiency—because it prevents jostling and saves time.

The analogy, which has just been drawn between the basidia on a hymenial area coming to maturity in successive generations and the soldiers in a battalion passing a given point in the line of march, is only a rough one and fails in certain details. Thus, on any hymenial area, there is a wave of development (the details of which have already been discussed) of such a nature that the basidia of the present generation, proceeding from one side of the area to the other, unlike the leading four in a column-of-fours of a battalion, are progressively more and more advanced. Other defects in the analogy we need not discuss.

We have seen that on each gill developmental waves pass over the hymenium in an irregular manner: they clash and meet one another in a way which can only be determined by observation; and to these waves the phenomenon of mottling is due. What advantage, if any, is there in the existence of these waves? With the wave-system of organisation we find that there are present on the gill a large number of hymenial areas in different stages of development: there are not only black, brown, and white areas, but even the areas of one kind, *e.g.* the black areas, do not keep developmental time, for some of them shed their spores sooner than others. The general want of synchrony between the areas is advantageous to this extent, that it enables the fruit-body as a whole to shed spores not intermittently, in discontinuous showers, but in a constant stream. Very many plants which produce a large number of organs of dissemination have arrangements which secure that these organs shall be gradually and not simultaneously set free. Thus in many Mycetozoa, Liverworts, and Puff-balls, elaters or capillitium threads are present from which the spore-dust only disentangles itself with difficulty with the passage of time; and even in the capsules of certain Orchids elater-like hairs play a similar rôle in the dispersal of the seed-dust.[1]

In this connection one may also cite the capsules of Epilobium, Salix, Populus, etc. These, which contain many small seeds, open

[1] E. Pfitzer, in Engler und Prantl, *Pflanzenfamilien*, Teil II, Abteilung 6, *Orchidaceae*, 1889, p. 73.

from the apex downwards and so allow their seeds to escape in succession. A gradual dispersion, as opposed to a simultaneous one, seems to result in a greater chance of wide distribution for the spores or seeds of any individual plant, owing to the fact that external conditions, such as the direction of the wind, rain-fall, presence of animals, etc., are constantly changing. Now let us suppose that the basidia of the first generation of a fruit-body of *Panaeolus campanulatus* were to begin the development of their sterigmata at exactly the same time. Then, for eight hours afterwards, no spores would be shed. Then, suddenly, millions of spores would be liberated simultaneously. Let us further suppose that the basidia of the second and of all the succeeding generations were to develop synchronously. Then spore-discharge would take place as follows : millions of spores of the first generation set free simultaneously ; then a pause of about eight hours ; then millions of spores of the second generation set free simultaneously ; then another long pause ; and so forth. The irregular wave-method of hymenial development leads to an avoidance of this intermittency in spore-discharge. In nature, a fruit-body of *Panaeolus campanulatus* liberates spores gradually from the first moment of spore-discharge until its close. So many spores are set free each minute for from seven to ten days. The never-ceasing stream of spores which pours out from beneath the pileus during the whole period of spore-discharge is directly traceable to the lack of synchrony in the development of the numerous hymenial areas.

Upon a single gill of *Panaeolus campanulatus* there are between 500,000 and 1,000,000 basidia, the number varying according to the size of the pileus. An arrangement whereby all these basidia would begin and end their development exactly simultaneously for all of the series of generations into which they are divided would necessarily be complex. The protoplasm of the gill would require to act as a very perfect unit, the whole controlling each small part of the hymenium, if such perfect unison of development were to be attained. The physiological arrangements for the production of successive generations of basidia are perhaps more easy to carry out, *i.e.* require much less correlation of the protoplasmic mechanism involved, when numerous small areas of the hymenium can act

more or less independently of one another, as happens in *Panaeolus campanulatus*, than when all are required to act synchronously. An analogy may be drawn once more from the organisation of an army. It is no difficult matter for a battalion of soldiers to march in step and in proper order in ranks of four abreast, but it would be less easy, were the ranks composed of 16 men. Now imagine an army of 50,000 men all marching as massed formation across a piece of country together. The order of march might conceivably be 50 ranks of 1,000 men each, or it might be a parallel series of battalions say of 1,000 men each in which there are only 4 men in each rank in each battalion. Even if the country passed over were quite flat and presented no natural obstacles, with the first arrangement, *i.e.* 1,000 men to a rank, it would be extremely difficult for the ranks to be properly held. One part of a rank would tend to bulge forward in front of other parts, and the most exacting vigilance would be required by every soldier if the ranks were to be kept anything like straight. A much easier way of marching the army over the ground would be one commonly employed and already mentioned, namely, forming the army into battalions, arranging each battalion in a column-of-fours, and marching the battalions massed together more or less in parallel columns. Each battalion would have a certain amount of independence, and every rank could be properly held. This second method of organising the army is the one which is most nearly analogous to the arrangement for bringing the basidia to maturity in successive generations on a gill of *Panaeolus campanulatus*. Each area roughly corresponds to a single battalion acting more or less independently of its fellows.

In concluding this section, I wish to call attention to the interesting parallel which exists between the undulatory development of the spore-producing hymenium of *Panaeolus campanulatus* and the undulatory development of the epithelium which produces spermatozoa in the testicular tubules of the Mammalia. When one of these tubules, *e.g.* of a cat, is examined in a series of microtome sections, waves of developmental activity can be traced along it.[1]

[1] *Cf.* E. A. Schäfer, *The Essentials of Histology*, ed. 10, London, 1916, pp. 393, 395, Figs. 549, 552.

Here, in the tubule, all the spermatozoa appear to be quite ripe but are still held in place by the nurse cells (cells of Sertoli) in which they were nourished. A little farther along the tubule, the spermatozoa are being set free. Still farther along, it is evident that the spermatozoa have been recently liberated and that preparations are under way for the formation of their successors. Still farther along, a new crop of spermatozoa is partly developed. Still farther along, the spermatozoa are all ripe and thus resemble those which were first observed. Wave after wave may thus be traced in one and the same tubule ; and, doubtless, each part of every tubule produces a series of successive generations of spermatozoa. Thus the development of spermatozoa by the epithelium lining the tubules of the testis of a Mammal very much resembles in its time and space relations the development of basidiospores by the hymenium covering the flat and exposed gills of *Panaeolus campanulatus*. It seems, therefore, that the problem of efficiency in the production and liberation of vast numbers of minute organic particles has been solved in the same way by the higher animals and by a lowly toadstool. Just as a fruit-body of Panaeolus is organised so that, throughout its period of functional activity, it liberates a constant stream of millions of spores into the air, so the testis of a Mammal is organised so that, throughout its functional activity, it liberates a constant stream of millions of spermatozoa into its tubules. The spores are set free as soon as they are ripe, so that they may be scattered by the winds and thus find new substrata for the development of new individuals of the species. The spermatozoa, which are simply male gametes, are confined in a storage chamber and ever renewed, so that they may be always ready for employment in a sexual act.

The Spores which are Wasted.—Whenever one examines a fruit-body of one of the Hymenomycetes at the end of the spore-discharge period, one finds that it has adherent to its gills a considerable number of spores which for some reason or other have failed to be properly liberated. These spores, since they contribute nothing to the dispersal of the species in nature, may be called *wasted spores*.

We are now acquainted with the fact that the production and liberation of spores is the outcome of a number of complicated developmental changes. Let us recapitulate the more obvious of these changes in so far as they concern the basidium. A basidium, on beginning to mature, grows in length and volume, and at the same time gradually fills with protoplasm. On attaining full size, its two nuclei unite. The fusion-nucleus then forms four daughter nuclei by two successive karyokinetic divisions. Then the four sterigmata are brought into existence, and afterwards the spores. The four nuclei then creep up, or are drawn through, the sterigmata into the spores, so that each spore comes to have one nucleus only. For some hours the basidium pours cytoplasm and food materials into the spores, so that in the end the spore-contents become very dense indeed. The metabolism taking place in a maturing spore involves, among other processes: the temporary production of glycogen, the thickening of the cell-wall, and the manufacture of a brown pigment; and a mature spore excretes a tiny drop of water from its hilum just prior to its being forcibly shot away from its sterigma. Each spore, immediately after being discharged, provided that no hindrance arises from misplaced gills, creeping insects, violent winds, etc., escapes down an interlamellar space into the free air beneath the pileus and is then carried off by the wind. It would be astonishing, if, in view of all the complex changes which take place during the production and liberation of spores, every spore out of all the millions produced were to succeed in escaping from a fruit-body. As a matter of fact, a considerable number of spores is always wasted. These victims of some accident, which has occurred either during development or discharge, adhere most tenaciously to the gills and only reach the earth when the fruit-body which has produced them collapses and undergoes putrefaction at the end of the spore-fall period.

While the absolute number of spores which are wasted is frequently large, often amounting to several millions, the ratio of the wasted spores to the whole number produced may be small. It is well to bear this in mind: otherwise it may be thought that the wonderful arrangements for securing the successive production of mature basidia are to a large extent rendered nugatory by an

inefficient mode of spore-discharge. We shall now study the wasted spores a little more closely. We shall first estimate their number, and then pass on to discuss a curious accident which may befall them at the moment when they should be liberated.

In order to find out the number of wasted spores which may be present on a fruit-body of *Panaeolus campanulatus*, a culture of this species was made on horse dung in the laboratory under a large bell-jar. The first large fruit-body which came up was chosen for observation. During its spore-discharge period, which lasted about ten days, care was taken not to disturb it in any way. As soon as the spores had ceased to be liberated, the exhausted gills were examined under the microscope. A *camera-lucida* sketch of all the collapsed basidia and of all the wasted spores was made for an area of the hymenium which just filled the field of view (Fig. 103). The number of wasted spores was easily counted. The total number of spores which the whole area had produced was evidently equal to the number of sterigmatic stumps, and it was obtained by counting the exhausted basidia and multiplying the number found by 4. The total number of spores produced on the area was 1,832, of which 70 had been wasted. The wasted spores, therefore, formed only 3·8 per cent. of the whole number produced. In respect to the number of wasted spores, the area chosen for investigation was, so far as I could judge from inspection, of average character. Some areas, however, were richer in wasted spores and some poorer. In one of the poorer fields, which was equal in extent to the one already illustrated, only a single wasted spore could be observed, and in another only 15. From the results of these observations I think it would be safe to say that, for the fruit-body investigated, the wasted spores were approximately from 3 to 4 per cent. of the whole number produced.

By tracing the outlines of the gills removed from one quarter of the pileus and measuring their superficial areas, both sides of each gill being taken into account, it was calculated that for the whole pileus:

the 60 long gills had a superficial area of about 60 square cm.,
the 60 intermediate gills had an area of about 24 square cm.,
the 120 short gills had an area of about 4 square cm.,

and consequently the area of the hymenial layer of the whole fruit-body was approximately about 88 square cm.

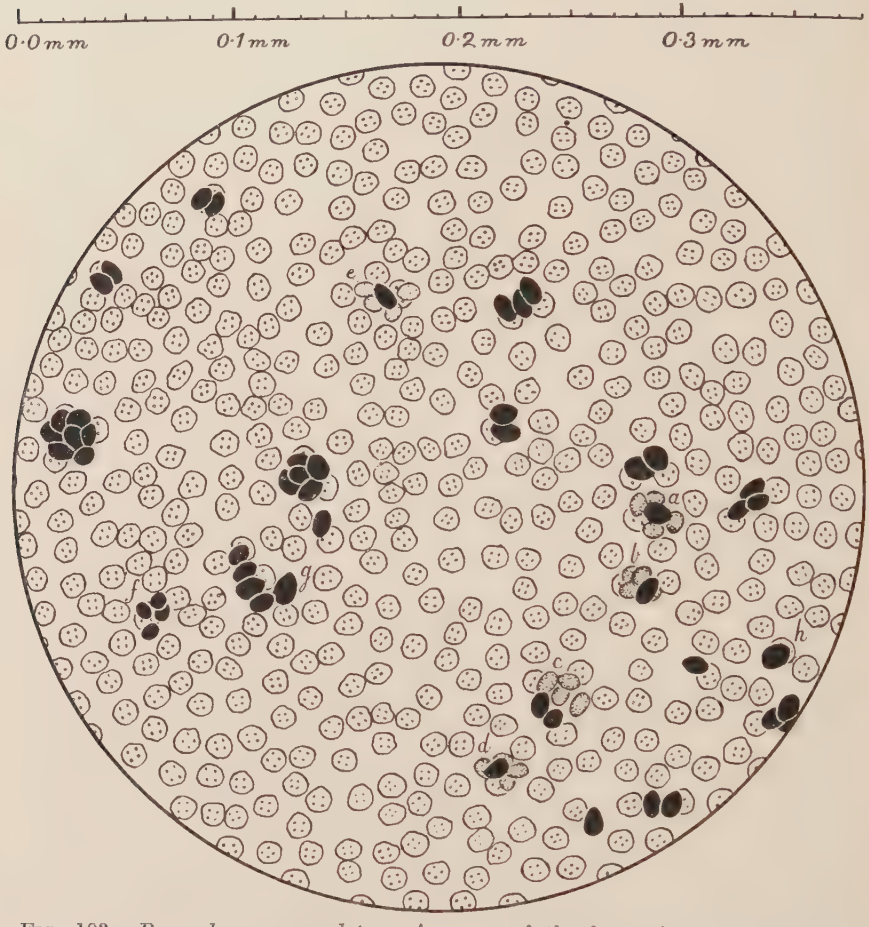


Fig. 103.—*Panaeolus campanulatus.* An area of the hymenium equal to one-seventh of 1 sq. mm., drawn after spore-discharge had ceased, showing the exhausted basidia and the wasted spores. The paraphyses are omitted. Most of the spores left lying on the hymenium were black. Four sets of spores, *a*, *b*, *c*, and *d*—each set of four the product of a single basidium—were brown, and one set, *e*, colourless. The four black spores at *f* are abnormally small, and the single spores at *g* and *h* abnormally large. The number of sterigmatic stumps on the exhausted basidia indicate that the area produced 1,832 spores. The wasted spores number 70, *i.e.* 3·8 per cent. of those produced. Magnification, 293.

On 0·01 square mm. of an exhausted hymenial area the number of basidia was found to be 61. It was therefore calculated that

the number of basidia on a square mm. was about 6,100 ; on a square cm. 610,000 ; and on 88 square cm., *i.e.* on all the gills taken together, 53,680,000. From this, reckoning four spores to each basidium, it was calculated that the total number of spores which the fruit-body had produced was approximately 215,000,000. If we take the number of wasted spores as forming 3·8 per cent. of this number, the absolute number of wasted spores on the whole fruit-body was about 8,000,000. Subtracting this from the whole number of spores produced, we find that 207,000,000 spores were liberated. We may conclude, therefore, that even when the wasted spores left on the gills amount to millions they may yet be very few compared with the vast number which have been set free.

We may now enquire into the causes which may prevent full-grown spores from being properly liberated. If a gill is displaced so that its median plane is no longer vertical but inclined at an angle of several degrees, then a spore which has been shot out at one point on the upper side of the gill will soon strike the gill again at a lower point. After falling on a gill in this way, a spore never gets free again : it adheres tightly to the hymenium until the fruit-body decays. An illustration showing the effect of inclining gills shaped like those of *Panaeolus campanulatus* has been given in Volume I, Fig. 12, p. 40. When a large number of spores fall on to the upper side of the gill of a displaced fruit-body, the gill on its upper side becomes, in the words of the field-botanist, "powdered with the spores." In the fruit-body of *Panaeolus campanulatus* which was investigated the median planes of the gills were properly adjusted in space, so that this powdering could not occur.

On almost all large fruit-bodies of Hymenomycetes growing in woods in the warm days of autumn one may find Fungus Gnats, Mites, or Springtails. These crawl over the gills. Doubtless they displace many of the spores, for they are bound to touch these in their peregrinations. However, the extent to which crawling insects are a cause of the accumulation of wasted spores on gills, etc., in nature, requires further investigation. So far I have made no special observations in connection with this matter.

When the wind is blowing strongly in one direction, the spores,

when about to pass out from between the interlamellar spaces into the open air at the base of the pileus, may be blown on to the edges of the gills and stick there. In this way a certain number of spores is often wasted. I have noticed this phenomenon in connection with specimens not only of *Panaeolus campanulatus*, but also of *Anellaria separata* and a number of other species growing

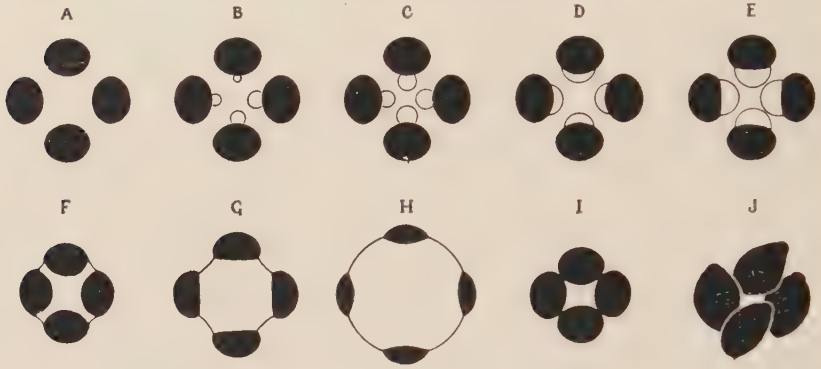


Fig. 104.—*Panaeolus campanulatus*. Excessive excretion of water-drops and the non-discharge of spores. A, four ripe spores of a basidium seen from above; B, the same excreting drops of water from their hila; C, the drops have attained full normal size (spores are usually shot away at this stage); D, the drops have become supernormal and have stepped up on to the sides of the spores; E, the drops are still increasing in size and now almost touch; F, the drops have fused and the spores have been dragged together; G, excretion of water has continued and the spores in consequence have become separated to the normal extent (*cf.* A); H, owing to a further excretion of water the spores have been pushed more than the usual distance apart; I, excretion has ceased, the water has evaporated, and the spores have been dragged together so that they adhere to one another; J, the basidium has collapsed and has dragged its four spores to the surface of the hymenium to which they now adhere and from which they cannot escape. Magnification, 660.

in the open. The edges of the gills of Panaeoli sometimes become quite black with the spores.

Probably the chief cause of the accumulation of wasted spores on gills is a failure in the discharging mechanism. The nature of this mechanism has so far defied exact analysis.[1] However, just before a spore is to be discharged, as was explained in Chapter I, a drop of water is exuded at the neck of the sterigma (Fig. 104, A, B, and C). When this drop has reached a certain definite size (C), the spore is shot away from the sterigma and bears the drop

[1] For a discussion of this mechanism *vide* Chap. I, pp. 22–26.

with it. Now, as I have observed when watching the discharge of spores with the horizontal microscope in the manner already described,[1] it sometimes happens that the spores on a basidium are not shot off when the drops below them have attained their normal size, but the drops increase in size (D and E) until they finally meet and fuse together (F). The four spores, without being detached from their sterigmata, are drawn nearer together owing to the pull exercised upon them by surface tension (F). The drops may go on enlarging so that the spores are pushed further apart than they are normally (G and H). The excretion of water by the sterigmata then ceases and the drop gradually evaporates. As the drop diminishes in size, the four spores are drawn together so that they come in contact with one another (I). A few minutes after the spores have met, the basidium to which the spores belong contracts in length, its end becomes concave, and its sterigmata are drawn into the concavity. It thus comes about that the four spores are dragged down to the general level of the hymenium, where they remain until the decay of the pileus sets in (J). The loss of spores owing to over-enlargement of the water-drops in the manner described was observed a great many times on the gills of *Panaeolus campanulatus* when they were being viewed with the horizontal microscope, but I have also observed the phenomenon on the gills of several other Hymenomycetes.

Sometimes, after two or three of the spores of a basidium have been successfully discharged, the remaining spores stay on their sterigmata until the basidium collapses. At the necks of the sterigmata belonging to the spores which are to be wasted no drops of water appear. In these cases the failure of the spores to leave their sterigmata may be connected in the first place with the failure in the excretory activity of the sterigmata. I have now watched the discharge of many hundreds of spores of different Hymenomycetes with a sufficiently high power of the microscope, but never once, since I began to pay attention to the excretory phenomenon, have I ever seen a spore shot away without a water-drop being formed, a few seconds before discharge, at the hilum of the spore where this is attached to the neck of the subjacent

[1] Pp. 260–263, also Figs. 91 and 92.

sterigma. My observations therefore seem to warrant the conclusion that the excretion of a water-drop is in some way absolutely necessary for the discharge of the spores in Hymenomycetes. Non-excretion and excessive excretion of water at the sterigmatic neck appear to be equally fatal to the spores concerned: both lead to the turning of normal-looking spores into wasters. In *Panaeolus campanulatus* I believe that the formation of many of the wasters is connected with the non-excretion of the water-drop.

Some of the waste spores, as judged by their size or colour or both, are evidently very immature (Fig. 103, *a*, *b*, *c*, *d*, *e*, p. 306). For some reason or other their development proceeded to a certain point only and was then inhibited. One could hardly expect such unripe spores to be shot away, for probably the development of the mechanism of discharge is connected with the final stages of ripening of the spores.

Among the waste spores one often finds some which are unusually large or unusually small or misshapen (Fig. 103, *f*, *g*, *h*). Clearly these are abnormal spores. The forces which cause a spore to become monstrous may also interfere with the discharging mechanism.

Sometimes one finds a little heap of wasted spores. In such a case it would seem that several adjacent basidia have failed in spore-discharge, and have each contributed spores to the heap. The spores of two basidia belonging to two successive generations may become stuck together so as to form a little group of eight. Smaller or larger groups of wasted spores may be formed by slight variations of this process.

Significance of the Protuberancy of Mature Basidia.—It has been pointed out that a basidium, when beginning to get ready to produce spores, grows in length until it protrudes a certain distance above the general level of the hymenial surface. The amount of the protuberancy thus attained will be at once realised by reference to Fig. 96 (p. 287). After the basidium-body has reached its full length, then, and then only, are the sterigmata developed; and only when the sterigmata have been pushed out to their full extent do the spores begin developing at their ends.

The phenomenon of protuberancy, as will be shown in detail

in Volume III, is most marked in the various species of Coprinus, but it is also very strikingly displayed in *Lepiota cepaestipes* and *Psathyrella disseminata*. In the fruit-bodies of all these species, the basidia can be separated into different classes according to their length ; and, in a single species, they are dimorphic, trimorphic, or quadrimorphic. Subsequently it will be shown that the differential protuberancy, where polymorphism of the basidia occurs, is correlated with the crowding of the basidia and is necessary to prevent the spores of adjacent basidia from touching one another and sticking together. For the present, therefore, let us take it for granted that basidial protuberancy, where most strongly developed, is evidently related to the mechanical requirements of the spores, *i.e.* to the provision of a free space for spore-development and spore-discharge.

In the fruit-bodies of the Panaeolus Sub-type the basidia are monomorphic, *i.e.* when mature they are all about equally protuberant beyond the general level of the hymenium. The question arises : why should these basidia be protuberant at all ? I shall attempt to answer this question in connection with *Panaeolus campanulatus*. First, it is to be remarked that the protuberancy of any basidium in the hymenium is strictly temporary : it is acquired shortly before the development of the spores, and lost almost immediately after the spores have been discharged. Evidently, basidial protuberancy is connected with the development and discharge of the spores. It seems to me that the lengthening of the maturing basidia, which results in their becoming protuberant, is of considerable advantage to the functional activity of the fruit-body in the following respect : it causes the spores, which develop on the basidia only after these have become protuberant, to take their origin, grow to maturity, and be discharged above the general level of the hymenium in spaces which are mechanically free from neighbouring hymenial elements.

We have seen that, owing to various imperfections, a certain number of spores, instead of escaping freely from a fruit-body, become wasted in that they stick tenaciously to the hymenium. Now there is always some danger that the waste spores of one generation may become obstacles to the development, and particularly

to the discharge, of the spores of subsequent generations: but, owing to the fact that maturing basidia become protuberant and develop their sterigmata before they develop their spores, this danger is reduced to a minimum. With the horizontal microscope, when watching the coming into existence and disappearance of successive generations of basidia, I several times saw that a maturing basidium, during its development, pushed aside one or more of the waste spores which had overlain it or had been in contact with it. The result was that the sterigmata were reared above the hymenium in a free space, and that the new spores were developed free from all obstacles. The practical advantage of protuberancy thus became a matter of observation. Even when a hymenium is thickly strewn with wasted spores, a considerable number of basidia succeed in pushing up between the obstacles in their way and in raising the tips of their sterigmata into freedom in preparation for spore-development.

Significance of the Collapse of Exhausted Basidia.—It has been pointed out that, some fifteen to thirty minutes after a basidium has shed its four spores, the basidium-body contracts in length so that it ceases to be protuberant (*cf.* Fig. 93, A, p. 272, and Fig. 98, A and B, p. 292), and that at the same time the sterigmata become drawn into the concavity which is formed at the basidium-body end. It might be argued that the rapid collapse of a basidium which has shed its spores is simply due to the fact that the basidium is exhausted. In support of this one might urge that the protoplasm in a basidium which has shed its spores is devoid of nuclei and extremely small in amount, and also that, since such a basidium has no further function to perform, its death might well be expected to take place just when it actually does. However, while all this may be true, yet it is conceivable that a basidium should remain living long after it has discharged its spores. Masses of cytoplasm separated from all nuclear influence, as we know from actual experiments with Amoebae and the cells of the Higher Plants, do not necessarily die immediately after their isolation. If it were for the advantage of the hymenium that basidia which have shed their spores should remain protuberant and turgid, it seems to me very likely from

analogy that we should find this arrangement in existence. However, the rapid collapse of basidia which have shed their spores, whatever its physiological cause, fits in very well with the general organisation of the hymenium. It would be distinctly disadvantageous for exhausted basidia to remain protuberant, owing to the fact that their sterigmata, and any undischarged spores which they might carry, would be liable to be in the way of the new spores in course of development or discharge. By their rapid collapse after shedding their spores, basidia get rid of their sterigmata entirely, and they also drag down any spores, which they have not succeeded in discharging, to the general level of the hymenium. After having been brought to this low level, these wasted spores are mechanically harmless ; for, as we have seen, maturing basidia, when elongating, push them aside without difficulty. The rapid collapse of exhausted basidia is therefore significant from the point of view of the organisation of the hymenium as a whole, in that it leads to the rapid removal of useless sterigmata and wasted spores from positions where they might form mechanical hindrances to the development and discharge of the spores of later basidial generations.

The Relative Position of the Basidia and the Spores of One Generation.—The distribution of the basidia belonging to a single generation is shown for *Panaeolus campanulatus* in Figs. 89 (p. 257) and 90 (p. 258). It follows no precise mathematical rule. However, one can see from inspection that the basidia are separated from one another by such distances that their spores cannot come into contact with one another : mutual interference is rendered impossible. At the same time the basidia are sufficiently evenly spread over the hymenium, and sufficiently near to one another, to prevent there being any great waste of space. The distances separating the basidia are usually confined within fairly definite and circumscribed limits. If one considers the area shown in Fig. 89 (p. 257), one sees that there are not many places where one could insert additional spore-bearing basidia without reducing to a dangerous minimum the margin of safety for securing the isolation of the spores of each basidium. We may conclude that, for *Panaeolus campanulatus*, the distribution of the basidia of any

one generation over the hymenium is economical, in that the basidia are crowded as closely as is consistent with the conservation of that mechanical freedom which is required for the proper development and discharge of the spores.

Exceptions to the rule just given certainly occur. One sometimes finds that, here and there on the hymenium, a few of the basidia are more closely crowded than they are in the areas represented in Figs. 89 and 90. Occasionally, two spores, one belonging to one basidium and the other to another, are so close to one another that they almost touch (Fig. 112, *F*, p. 323). In some rare instances even, actual contact may be observed (Fig. 112, *D*). Sometimes also it happens that here and there the basidia are distinctly more loosely scattered than is necessary for the safety of the spores. That such imperfections in distribution should sometimes make themselves manifest is not to be wondered at, when one reflects that a single fruit-body of *Panaeolus campanulatus* may in the course of its development produce some 50,000,000 basidia.

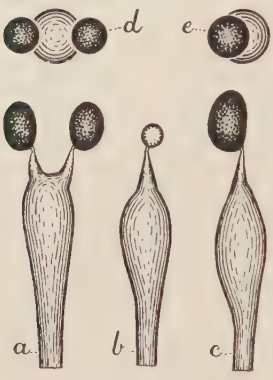


FIG. 105.—*Psalliota campestris* (cultivated). *a*, a normal disterigmatic basidium; *b*, a young monosterigmatic basidium; *c*, a mature monosterigmatic basidium; *d* is *a* seen from above; *e* is *c* seen from above. The spore of *c* is about twice the volume of one of the spores of *a*. Magnification, 1,060.

The Position of the Sterigmata in the Hymenomycetes generally and in Panaeolus campanulatus.—First let us consider the position of the sterigmata on a single basidium in the Hymenomycetes generally. In the vast majority of species the number of sterigmata on the end of each basidium is normally four. However, there are some species in which the basidium has only one sterigma, others in which it has two sterigmata, others in which it has three, others in which it has six, and yet others in which it has eight. Further, in a species in which the number of sterigmata is normally four, occasionally one may find basidia with three or five sterigmata; and, where the number is normally two, monosterigmatic basidia are usually frequently present. Probably

in all species occasional variations from the normal number of sterigmata occur, and in this respect basidia may be likened to certain compound leaves and flowers of the Phanerogamia, where analogous variations in the number of the elements are not infrequent. We will now discuss the arrangement of the sterigmata in the different types of basidia, beginning with the simplest.

Monosterigmatic basidia, according to Patouillard, occur normally in *Pistillaria maculaecola* Fckl. and also in the Gastromycete *Hydnangium monosporum* Boud. et Pat., whilst in *Pistillaria fulgida* Fr., although the basidia are usually monosterigmatic, occasionally they are disterigmatic.[1] I myself so far have not examined these species. However, I have observed monosterigmatic basidia in the cultivated Mushroom, *Psalliota campestris*[2] (Fig. 105), and in *Coprinus bisporus* Lange (Figs. 106 and 107). In both these species the basidia are normally disterigmatic, but monosterigmatic basidia occur as by no means infrequent exceptions. Where a basidium is monosterigmatic, the sterigma always occupies a central position at the top of the basidium (Fig. 105, *b* and *c*). The spore, however, is not symmetrically set on the end of the sterigma, but is attached unilaterally in the manner which is characteristic of the spores

FIG. 106.—*Coprinus bisporus*. Two fruit-bodies growing on a stick sent from Kew. The disc remains prominent until exhaustion of the pileus. Photographed at 10 A.M. at Winnipeg. Natural size.

[1] N. Patouillard, *Tabulae analyticae fungorum*, sér. 1, 1883–1886, nos. 47, 50, 692.

[2] *Vide infra*. Monosterigmatic basidia are shown for the Mushroom in Figs. 146 and 147, Chap. XIII.

of tetrasterigmatic basidia (Fig. 105, *b*, *c*, *e*; *vide* also basidia nos. 48 and 57 in Fig. 147, Chap. XIII).

Disterigmatic basidia have been observed by me as normal in

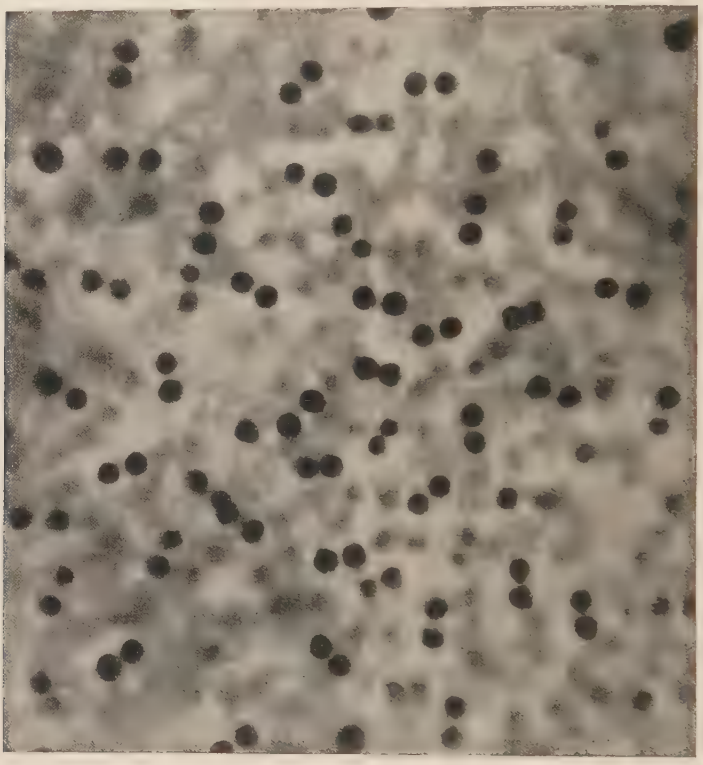


Fig. 107.—*Coprinus bisporus.* Photomicrograph of a portion of the hymenium in surface view. The spores of the long basidia only are in focus, but those of the short basidia can be faintly seen out of focus. All the basidia, except three, bore two spores. The three exceptions (one at the right top corner, one below the left top corner, and one in the middle of the lower edge) each bore one spore of large size. Magnification, 480.

a form of *Mycena galericulata*, in the cultivated forms of *Psalliota campestris* (Fig. 105), in *Coprinus bisporus* (Figs. 106 and 107), *Galera hypnorum*, *Hygrophorus conicus*, and *Calocera cornea*. They occur too, as the literature of mycology shows, in a number of other species, *e.g.* *Amanita bisporigera* Atkinson,[1] *Pistillaria*

[1] C. E. Lewis, "The Development of the Spores in *Amanita bisporigera*," *Botanical Gazette*, 1906, pp. 348–352.

micans Fr.,[1] *P. sagittaeformis* Pat.,[2] *P. Helenae* Pat.,[3] *Clavaria cinerea* Fr.,[4] *Hygrophorus agathosmus*,[5] *Pholiota togularis*,[6] *Tubaria conspersa*,[7] and *Corticium commixtum* v. H. et L.[8] When the whole number of Hymenomycetes is considered, the species with disterigmatic basidia are relatively few. However, these exceptional species are scattered through a considerable number of genera from the highest to the lowest. Possibly, when a sufficient number of critical studies has been made, it will be found that almost every large genus of the Hymenomycetes has one or more species which normally have disterigmatic basidia. In *Amanita bisporigera*, *Coprinus bisporus*, and *Psalliota campestris*, there can be but little doubt that the two-spored condition has been obtained by reduction from the four-spored, and possibly this is true in all disterigmatic species. The suppression of two sterigmata out of four may be likened to the suppression of spines in the Prickly Opuntia and the suppression of colours in certain flowers. Evolution seems to have taken place by means of the loss of a character.

In disterigmatic basidia the two sterigmata are always set opposite to one another in a symmetrical manner, one on each side of the top of the basidium-body. At their origin, they seem to repel one another and thus come to be situated as far apart as possible (Fig. 105; also Figs. 146 and 147, pp. 416, 429).

Tristerigmatic basidia, so far as I know, are the rule for one species only. I have discovered that in *Coprinus narcoticus* (Fig. 108), the normal number of sterigmata for each basidium is three only. Mixed with the tristerigmatic basidia, however, are a certain number of tetrasterigmatic. The fruit-bodies used for my observations came up spontaneously in 1912 and again in 1922 in laboratory cultures of horse dung collected from the streets of Winnipeg. The species was readily recognisable from the first by the remarkably pungent odour of the pileus during autodigestion. A photograph of the hymenium seen from above

1, 2, 3, 4 N. Patouillard, *Tabulae analyticae fungorum*, sér. 1, 1883–1886.

5, 6, 7 V. Fayod, "Prodrome d'une histoire naturelle des Agaricinés," *Ann. sci. nat.*, 7 sér., T. IX., 1889, p. 262.

8 F. von Höhnel und V. Litschauer, "Beiträge zur Kenntnis der Corticieen," *Sitzungsb. der K. Akad. der Wiss. in Wien*, Bd. CXVI, 1907, p. 83.

is shown in Fig. 109. In many species in which the basidia are normally tetrasterigmatic one may sometimes find a few basidia scattered at rare intervals which are tristerigmatic. Such I have observed for example in several species of Coprinus, *e.g. C. niveus* (Fig. 110, *b*), in *Panaeolus campanulatus*, and in the field forms of *Psalliota campestris*.

Fig. 108.—*Coprinus narcoticus*—a Coprinus with a strong and disagreeable odour. Fruit-bodies coming up in a pure culture on horse dung. Species obtained at Winnipeg. Photographed at 6.30 A.M. The opening of the pileus takes place during the night. Natural size.

In tristerigmatic basidia the three sterigmata are always placed equidistantly at the top of the basidium. Their positions are like those of the three corners of an equilateral triangle.

Tetrasterigmatic basidia are the rule in most species of Hymenomycetes. This arrangement is so frequent that there is no need to quote the names of species. Wherever it occurs, the four sterigmata (except in certain Tremellineae) are placed equidistantly on the top of the basidium. Their relative positions are like those of the four corners of a square.

Pentasterigmatic basidia, according to Patouillard,[1] occur in *Cantharellus Friesii* Q. The illustration given by this author shows a single basidium with five sterigmata and five spores. In *Anellaria separata*, *Coprinus niveus*, and some other species of Agaricineae, where the basidia are normally tetrasterigmatic, I have occasionally met with a basidium with five sterigmata (Fig. 110, *c*). In pentasterigmatic basidia the sterigmata have the same relative positions as the five corners of a regular pentagon.

[1] N. Patouillard, *loc. cit.*, p. 148.

Abnormalities in the basidia of *Coprinus niveus* include not only tristerigmatic and pentasterigmatic basidia, but also spores which exhibit equal or unequal bifurcation to a greater or less degree. Some of these curious spores are illustrated in Fig. 110.

Hexasterigmatic basidia occur in *Sistotrema confluens* Fr.,[1] *Cantharellus cibarius*, and some other species of Cantharellus.[2] Basidia with six sterigmata are also not infrequent in *Exobasidium vaccinii*[3] and some species of Corticium.[4] The bases of the sterigmata for each basidium have the same relative positions as the corners of a regular hexagon.

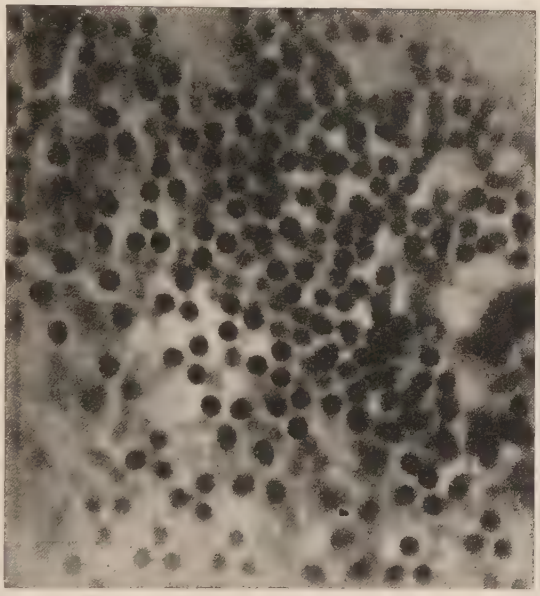


Fig. 109.—*Coprinus narcoticus*. Photograph of the hymenium, to show that the basidia are trisporous. The basidia, as in most Coprini, are dimorphic. The spores of most of the long ones only are in focus, and the spores of the short ones out of focus. There are three spores only above each basidium. In the middle of the right-hand side the spores were removed from their sterigmata during the making of the preparation. Magnification, 440.

Heptasterigmatic basidia, so far as I know, are not the rule in any of the species of Hymenomycetes. However, they occur exceptionally in some Thelephoraceae where the normal number of sterigmata is eight. I have not seen any such basidia myself but, doubtless, where they occur, the relative positions of the sterigmata are like those of the corners of a regular heptagon.

[1] N. Patouillard, *loc. cit.*, p. 111. [2] *Cf.* V. Fayod, *loc. cit.*, p. 262.

[3] N. Patouillard, *Essai taxonomique sur les familles et les genres des Hyménomycètes*, Lons-le-Saunier, 1900, p. 35.

[4] F. von Höhnel und V. Litschauer, *loc. cit.*, p. 84.

Octosterigmatic basidia occur in some of the Thelephoraceae, *e.g. Corticium coronatum* (Schröt.) v. H. et L. Here, according to von Höhnel and Litschauer,[1] almost always, eight sterigmata are present on each basidium. I myself have seen octosterigmatic basidia in one of the species of Corticium. In octosterigmatic basidia the sterigmata on the top of the basidium have the same relative positions as the corners of a regular octagon.

Fig. 110.—*Coprinus niveus.* Teratology of basidia and spores. *a*, a normal tetrasterigmatic basidium; *b*, a tristerigmatic basidium; *c*, a pentasterigmatic basidium; *d*, a normal spore seen from in front and sideways; *e*, *f*, and *g*, spores showing progressively deep bifurcation; *h*, a small spore showing bifurcation; *i*, *j*, and *k*, spores showing progressively asymmetrical bifurcation; *l*, an irregularly shaped spore; *m*, two very small black spores, one showing a bifurcation. Magnification: *a*, *b*, and *c*, 293; *d*–*m*, 707.

So far as I am aware, there are no species of Hymenomycetes in which the normal number of sterigmata on each basidium is nine, ten, or any regular number greater than eight.

From the foregoing, we have seen that, at their origin on the top of a single basidium, the sterigmata appear to repel one another with equal strength, so that in the end the spaces separating adjacent sterigmata are all equal. We may therefore state the following law with regard to the position of sterigmata on any one basidium: *When only one sterigma is present, it occupies a median position on the top of the basidium-body; when more than one sterigma are present, the sterigmata arise in such positions on the top of the basidium-body that they are as remote from one another as possible.*

From the observations of cytologists [2] it appears that the nuclei derived from the fusion-nucleus in the basidium attach themselves by means of their centrosomes to those parts of the basidial wall which are to bulge upwards and develop into sterigmata. We

[1] F. von Höhnel und V. Litschauer, *loc. cit.*, p. 94.

[2] *E.g.* M. Levine, "Studies in the Cytology of the Hymenomycetes, especially the Boleti," *Bull. Torrey Bot. Club*, vol. xl, 1913, pp. 172–173. For reference to the papers of René Maire and R. E. Fries, *vide infra*, Chap. XIII.

may therefore conclude that the positions of the sterigmata on the end of any basidium are decided by the positions of the nuclei in the basidium just before the sterigmata are formed.

The number of sterigmata on a basidium is doubtless related to the number or mode of arrangement of the nuclei derived from the fusion-nucleus. Probably in tristerigmatic basidia there are only three nuclei present instead of the usual four, while in pentasterigmatic and octosterigmatic basidia there may be five nuclei and eight nuclei respectively. If the fusion-nucleus divided three times, eight nuclei would result, and this may happen in octosterigmatic basidia; but how the fusion-nucleus divides so as to form only three nuclei or just five is rather puzzling. No doubt light might be thrown on this matter by cytological investigation.

FIG. 111.—*Coprinus echinosporus* Buller. Surface view of the hymenium showing plan of spores which have a domino-like arrangement, as in the lines *a–b* and *c–d–e*; *f*, a cystidium. The spores of the long basidia have been shaded, those of the short basidia left plain. The echinulations are only shown at *g* where two spores are represented in lateral view. Magnification, 440.

We have so far dealt with the position of the sterigmata on individual basidia. We shall now turn our attention to the position of sterigmata on closely adjacent basidia. In certain species of Coprinus, *e.g. C. echinosporus* Buller, if one examines the hymenium in face-view, one can at once observe that the spores of adjacent basidia tend to have the domino-eight arrangement (Fig. 111). If one had to crowd as many four-spored basidia as possible into a given area of the hymenium so that the spores would not touch one another, this could be done more successfully on the domino-eight plan than on any other. Proof of this is best obtained by

trial of different arrangements. In *Coprinus echinosporus*, therefore, the basidia mutually influence one another in the arrangement of their sterigmata so that in the end the most economical arrangement tends to be established. In *Panaeolus campanulatus* I have not been able to observe any tendency toward the domino-eight arrangement.

Whilst I have not been able to convince myself that in *Panaeolus campanulatus* adjacent basidia influence each other in respect to the places of origin of their sterigmata, yet, when two or more basidia are unusually crowded, it is evident that they accommodate themselves to one another by a suitable bending of the sterigmata. Evidence of this phenomenon is afforded by the eight *camera-lucida* drawings given in Fig. 112. At H are shown three basidia. The middle one, which is the youngest, is crowded in between the two others. Its two lateral spores are drawn together and its other spores are separated by more than the normal distance. The position of these four spores is determined by the bending of the sterigmata. One can at once perceive that the middle basidium has beautifully adapted itself to its crowded position. Had its sterigmata had their usual direction, so that the spores would have been at the corners of a square, actual contact of at least one of the spores with the spores of one of the neighbouring basidia would have taken place.

The bending of the four sterigmata, so that one pair is drawn nearer together and the other pair becomes more divergent, results in a rhomboidal arrangement of the four spores when these are seen from above. From the various drawings in Fig. 112, it becomes evident that the rhomboidal arrangement is adopted only under conditions of crowding, and in such a way as to allow of the spores of any basidium affected being situated more favourably as regards space among the spores of the surrounding basidia. In Fig. 112 at A, D, and F, the rhomboidal arrangement comes out clearly in groups of mature basidia. At A, its adoption results in larger spaces being placed between the spores of several pairs of adjacent basidia. At D and F, where the necessity for the rhomboidal arrangement is very great, this arrangement is very marked indeed ; but, at D, it has not been quite sufficient to prevent the rare

accident of actual contact of two of the spores. At B, C, E, and H, the spores are all young, for none of them have yet turned

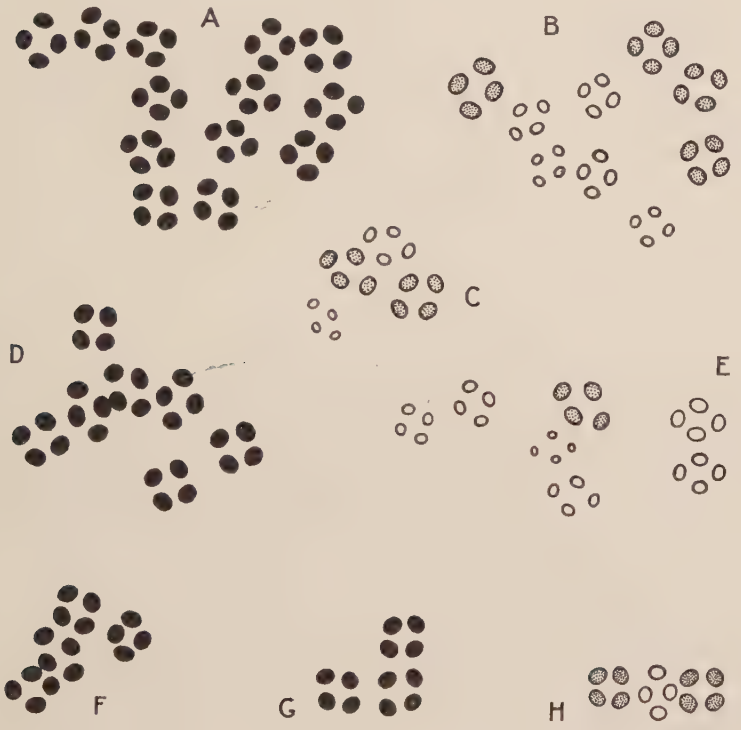


FIG. 112.—*Panaeolus campanulatus.* Studies of the relative positions of spores on adjacent basidia. As if to avoid jostling with the spores of adjacent basidia, the spores of certain basidia have a rhomboidal arrangement. This is clear in A, D, F, and H, where the spores have attained full size, but the phenomenon is also to be seen in B, C, and E, where many of the spores are only partially grown. In D, actual contact of two spores occurs, and in F is only just avoided. At G, the spores have nearly a domino arrangement. Ripe or nearly ripe spores are black, those full-sized and turning black are dotted, spores which are still colourless are unshaded. Magnification, 293.

black and some, indeed, have not yet attained full size. Yet, even here, the rhomboidal arrangement can be clearly seen. This shows that the sterigmata take up their final positions, so far as divergence is concerned, during their development, and further, that the sterigmata grow outwards in such directions that in the

end the spores will be placed in as favourable positions as possible. Evidently, *adjacent basidia exercise a mutual influence of a complex kind upon one another during development*: the two nearest sterigmata of two basidia which develop at the same time in close proximity tend to bend away from one another: when one sterigma of a basidium bends inwards toward the basidium-axis, the opposite sterigma bends inwards also, and at the same time the other pair of sterigmata become divergent as if repelled from the first pair. This results in the rhomboidal arrangement which can so readily be observed.

The Cheilocystidia.—In addition to the basidia and the paraphyses, the hymenium of many of the Agaricineae contains elements of a third kind which are known as *cystidia*. The cystidia are usually very protuberant, and are often considerably larger than either the paraphyses or basidia. They were originally called *cystidia* because they are often swollen and appear as cysts. Cystidia occur in the genera Coprinus, Pluteus, Inocybe, Russula, etc. Now the cystidia on the gills of many Agaricineae can be divided into two groups according to their location. Those which occur on the sides of the gills we may call *pleurocystidia* on account of their lateral position, whilst those which are present on the free lower edges of the gills we may call *cheilocystidia*. Some lamellate fungi possess both these kinds of cystidia, others one kind only, and yet others are lacking in both. *Panaeolus campanulatus* is unprovided with pleurocystidia, but possesses a considerable number of cheilocystidia. The free gill-margin of this species is devoid of basidia and therefore of spores, and the cheilocystidia are present in such large numbers that the gill-margin appears to the naked eye as a white line.

My investigations upon the cheilocystidia of *Panaeolus campanulatus* were made upon freshly-gathered fruit-bodies obtained from a grassy field in England close by a house which I was using as a laboratory. The fringe of cheilocystidia extends upwards above the extreme edge of the gills in some fruit-bodies to a maximum distance of 0·1 mm., but in others not so high. Each cheilocystidium has a somewhat swollen base embedded in the hymenium and is prolonged outwards beyond the general level of

the hymenium into a fine cylindrical hair, so that the whole cell is often 0·05–0·06 mm. long (Fig. 113, A). The tip of the cell usually excretes a drop of mucilage (B), and often the drops of neighbouring hairs become confluent, as is shown in Fig. 113 at C. Some of the largest drops, formed by the confluence of drops from about twelve cystidia, may be as much as 0·1 mm. wide and can just be distinguished by the naked eye. It was

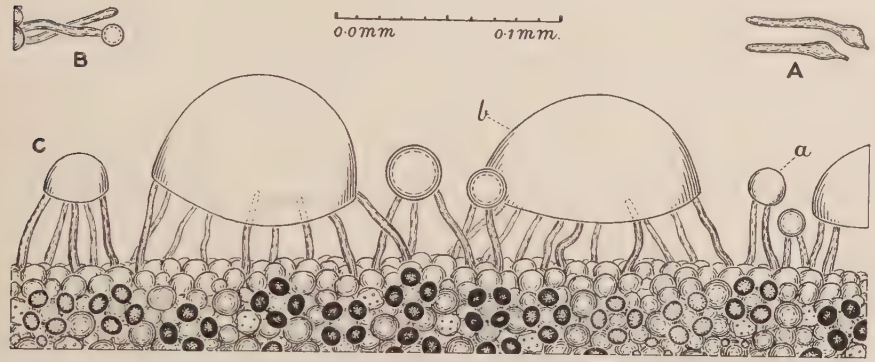


Fig. 113.—*Panaeolus campanulatus*. The cheilocystidia and their excretions. A, two young isolated cystidia. B, two cystidia projecting from a gill-edge, one of which has excreted a drop of mucilaginous fluid. C, part of the free lower margin of a gill, turned upwards and seen from the side, showing the hymenium on the side of the gill and the cheilocystidia projecting outwards from the gill-edge; *a*, a ball of mucilaginous fluid formed by the confluence of two drops excreted at the tips of two cystidia; *b*, a hemispherical mass of mucilaginous fluid formed by the confluence of about ten drops excreted at the tips of as many cystidia. Magnification, 293.

found that such drops tend to be plano-convex, apparently owing to the fact that the drops are unable to pass from the tips down the shafts of the cystidia (Fig. 113, C, *b*). When such a gill-edge as is shown in Fig. 113 is placed in water, the mucilaginous drops can still be seen for some time. They are not therefore immediately soluble in water. When exposed to air, the drops do not dry up anything like so quickly as would equally large drops of pure water. Knoll investigated similar hairs to these for several species of Agaricineae and came to the conclusion that they are hydathodes. He therefore called them *trichome-hydathodes*.[1] The

[1] F. Knoll, "Untersuchungen über den Bau und die Function der Cystiden und verwandter Organe," *Jahrb. f. wiss. Bot.*, Bd. 50, 1912, pp. 453–501.

extent, however, to which such organs reduce the amount of water in a pileus has not yet been measured. It is conceivable that the cheilocystidia are useful during the early development of the hymenium in removing from the gill-cells some of the superfluous water, and thus hastening the flow of nutrient substances which pour down the gill through the trama and subhymenium into the basidia.

CHAPTER XI

STROPHARIA SEMIGLOBATA

General Remarks—Description of the Hymenium in Detail—Rate of Discharge of the Spores of a Basidium and Collapse of the Basidium-body—The Spore-fall Period—Wasted Spores

General Remarks.—In this and the two following Chapters, we shall endeavour to extend our knowledge of the Panaeolus Subtype by studies made upon *Stropharia semiglobata*, *Anellaria separata*, and *Psalliota campestris*, the Common Mushroom.

Stropharia semiglobata is one of the commonest of field fungi. Like *Panaeolus campanulatus*, it is coprophilous and grows on horse dung in pastures throughout Europe and North America. Whilst wandering over grazing grounds at Sutton Park in Warwickshire, England, in the autumn, I have often seen hundreds of fruit-bodies on a single day. The fungus also occurs at Winnipeg and has come up spontaneously on horse dung which has been brought into the laboratory. There can be but little doubt that the spores of this species, like those of the Coprini and coprophilous fungi in general, are able to pass uninjured through the alimentary canal of horses and cattle. A proof of this statement, so far as horses are concerned, seems to be afforded by the following consideration. The winter at Winnipeg is so severe and prolonged that, for a period of about five months, no fungus can develop its fruit-bodies out-of-doors. In mid-winter, when horses drop their faeces on the snow in the open, the dung-balls immediately become frozen. Now, at this season, infection by air-borne spores of Stropharia is impossible since, owing to winter conditions, no such spores are being liberated. Yet, on several occasions, dung-balls, after having been collected in January or February in the frozen condition and set in covered crystallising dishes in the laboratory, have given rise in the course

of a few weeks to fruit-bodies of *Stropharia semiglobata*; and one such fruit-body is shown attached to its dung-ball in Fig. 114. It seems clear, therefore, that the spores of the Stropharia must have found their way into the dung-balls by passing down the alimentary canal with the hay.

FIG. 114.—*Stropharia semiglobata*. Photograph of a fruit-body grown on sterilised horse dung. Spores were being actively liberated under a bell-jar and some of them have settled on the annulus. Natural size.

A fuller explanation of the spontaneous development of the fruit-bodies on the dung-balls is as follows. The fungus comes up in the summer on dung dropped by herbivorous animals upon their grazing grounds. Hence the spores liberated from the pilei, after being carried by the wind, settle upon, and become adherent to, the surrounding grass. The grass in due time is made into hay and in this state is fed to horses in Winnipeg during the winter. The horses swallow the spores with their fodder, but the spores resist the action of the digestive juices and are in no way injured during their passage through the alimentary canal. The spores therefore become embedded in the dung-balls which, when dropped in the intensely cold air upon the frozen snow of the streets, freeze in the course of a

few minutes into solid masses. As soon as such frozen dung-balls are brought into the laboratory and thawed, the spores within them rapidly germinate and produce an extensive mycelium which, at the end of a few weeks, gives rise to fruit-bodies.

The mycelium retains its vitality in the dried condition for at least five months and probably much longer. I gathered some dung-balls in a field in England in August, 1911, allowed them to dry, and took them in the dried state to Winnipeg, where they were again moistened in January, 1912. A few days after the re-moistening, I observed that several fruit-bodies of *Stropharia semiglobata* had begun to come up on the dung. These grew rapidly in size and, at length, after elongating their stipes and expanding their pilei, began to liberate a cloud of spores. Thus convincing evidence was afforded that the mycelium of the fungus, after five months of quiescence in the dry dung-balls, had been able to resume its development in a normal manner.

The fruit-bodies of *Stropharia semiglobata* occur singly or in little groups, and occasionally two or three are joined at the base. In the wild state they are from 5 to 14 cm. in height, the cap 1 to 3 cm. broad, and the stipes, except for the somewhat swollen base, 2 to 4 mm. in thickness. Fig. 114 shows a fruit-body of large size grown in the laboratory, and Fig. 115 another fruit-body of about the maximum size which was gathered growing in a field in England. The outer surface of both the pileus and stipe are whitish yellow and very glutinous when moist. The fungus is regarded as poisonous.

The pileus is rounded at first but soon becomes semi-globate, from which shape it has received its specific name. It is smooth, with white flesh fairly thick at the centre and thinner toward the margin, even, viscous or very viscid when moist, but like smooth leather when dry. The viscid pellicle which is more or less transparent can be torn off the white flesh. It consists of hyphae the outer walls of which are gelatinous and confluent. The gills (Fig. 115, B) are adnate and squarely set against the stipe, often with a tiny decurrent tooth, broad, smooth, thin, and mottled purplish-brown. The spores in the mass are brownish-purple. The stipe is viscid in moist weather. Springtails which try to ascend it, as well as bits of grass-stems, etc., sometimes become stuck in

the gluten (Fig. 115, A). The annulus is situated not far below the pileus, is glutinous when moist, and sometimes (Fig. 114) becomes discoloured with spores which have fallen and lodged upon it.

FIG. 115. —*Stropharia semiglobata*. A fruit-body obtained from a field near Birmingham, England. A, shedding spores; B, in vertical section, showing mottling of gills. Natural size.

There is a general resemblance in the form of the fruit-bodies of a number of coprophilous fungi which grow on horse dung. Among these may be mentioned: *Panaeolus campanulatus*, *Stropharia semiglobata*, *Galera tenera*, and *Coprinus sterquilinus*. In each of these the stipe is much elongated relatively to the breadth of the pileus, thin, and hollow. Moreover, the stipes are usually attached at a low point in the substratum (Fig. 114). We seem here to have presented to us an adaptation to a coprophilous mode of life. The fruit-bodies arise at the base of dung-balls, so that they become the better attached; while a relatively long stipe is necessary in order that the pileus shall be brought out from between the dung-balls and raised well above the surface of the dung-ball heap. The stipes are thin, elastic, and hollow, so that with the least expenditure of material the maximum of rigidity is attained. In

Fig. 114 the lashing of the stipe to the side of a dung-ball for a distance of about 2 cm. by means of mycelial hyphae can be clearly observed.

The gills of *Stropharia semiglobata* possess all the characters of the Aequi-hymeniiferous Type, *i.e.* they are wedge-shaped in cross-section and positively geotropic, so that the hymenium everywhere looks more or less downwards toward the earth ; and every part of the hymenium of each gill actively produces and liberates spores during the whole period of spore-discharge. The gills also exhibit all the characters which have been enumerated for the Panaeolus Sub-type, as is indicated superficially by the mottling, which differs but little from that of *Panaeolus campanulatus* (Fig. 115, B). Whereas the spores of the Panaeolus are black, those of the Stropharia are purplish-brown. The dark areas of the latter fungus are therefore necessarily not so dark as those of the former.

Description of the Hymenium in Detail.—In Fig. 116 is shown a portion of the mottled surface of a gill actively engaged in producing and liberating spores. In the centre is a white area which, as indicated by the dotted lines and arrows, is enlarging itself centrifugally at the expense of the two dark areas. The two waves of development are proceeding in opposite directions. Only the spores have been drawn : those shown black are pigmented purple-brown, whilst those shown white are very young and possess walls which are still colourless. The preparation from which the drawing was made was obtained by removing a gill from a living fruit-body growing on horse dung in the laboratory, laying the gill flat on a glass slide, and covering it with a cover-glass without the use of any mounting fluid. During the few minutes while the drawing was being made with the *camera lucida*, the basidium *e* collapsed and dragged down its spores on to the hymenium. The spores of *d*, *f*, *h*, and *i* were also dragged down in a similar manner but have been represented as they were first observed. Under normal conditions there is no doubt that all these spores would have been shot out into an interlamellar space and would have escaped from the fruit-body. At *c*, when the drawing was begun, two of the four spores had already been discharged and at *d* one of the spores. From other observations, shortly to be recorded, one may conclude :

(1) that the full-sized spores, shown at *j* in the white area *a–b*, are a little more than an hour old ; (2) that the partially-grown spores near *b* are only a few minutes old ; and (3) that the oldest spores in the two dark areas are those nearest to the dotted lines, their age being about five hours and thirty minutes.

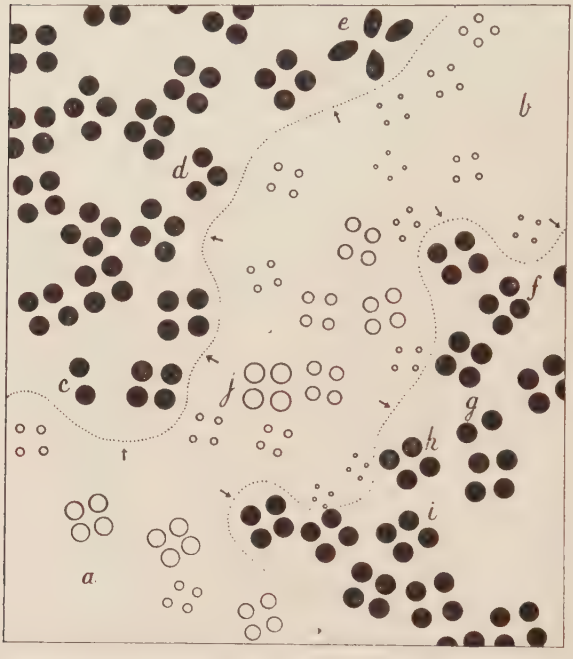


Fig. 116.—*Stropharia semiglobata*. Surface view of hymenium of a young fruit-body showing part of a white area, *a–b*, separating two black areas. The white area is enlarging at the expense of the black areas : it is progressing by two waves indicated by the dotted lines and arrows. The basidia *c*, *d*, and *g* had already shed some of their spores when the sketch was begun. Whilst the sketch was being made, the basidium, *e*, collapsed and dragged down the spores on to the hymenium. The spores of *d*, *f*, *h*, and *i* were also dragged down in a similar manner. Under normal conditions, all these spores would have been shot away into the interlamellar spaces. *j*, the oldest spores in the white area, possibly an hour old since their growth began. The spores in the white area which are still only partly grown are only a few minutes old. Magnification, 293.

A *camera-lucida* drawing showing the spores from the middle of a large black area is given in Fig. 117. From this it may be observed that the basidia of the present generation are fairly compactly arranged, but that any one basidium is sufficiently far from its nearest neighbours to prevent the risk of its being mechanically interfered with during the production and liberation of its spores. The rhomboidal arrangement of the four spores, the meaning of which was explained in connection with *Panaeolus campanulatus*,[1] often occurs in *Stropharia semiglobata* and

[1] Chap. X, pp. 322–324.

is well exhibited for the spores of a basidium just to the left of the middle of the Figure.

By the same methods as those which were employed for *Panaeolus campanulatus*, the hymenium of *Stropharia semiglobata* has been analysed in detail. At A, B, and C in Fig. 118 are represented pieces of the hymenium of a fruit-body which had been shedding spores for one, two, and about six days respectively. We thus have presented to us a series of illustrations of the hymenium showing its gradual exhaustion, which is complete at C. A day was reckoned as 24 hours, and only such elements were drawn as could be clearly perceived with the microscope. The cells of the hymenium can be divided into the following six classes: (1) *past-generation basidia*, *a a*, everywhere distinguished by their being collapsed, non-protuberant, and devoid of protoplasmic contents, and by containing sterigmatic stumps within their concave tops; (2) *present-generation basidia*, *b b*, fully protuberant, with the maximum diameter, and each bearing four spores into which the protoplasm is passing or has passed; (3) *coming-generation basidia*, *c c*, fully protuberant, with the maximum diameter, densely filled with protoplasm, lacking spores, but either with sterigmata, as in B, or without them, as in A; (4) *future-generation basidia*, *d d*, non-protuberant, with less than the maximum diameter, filled with fine protoplasmic contents, and lacking both sterigmata and spores;

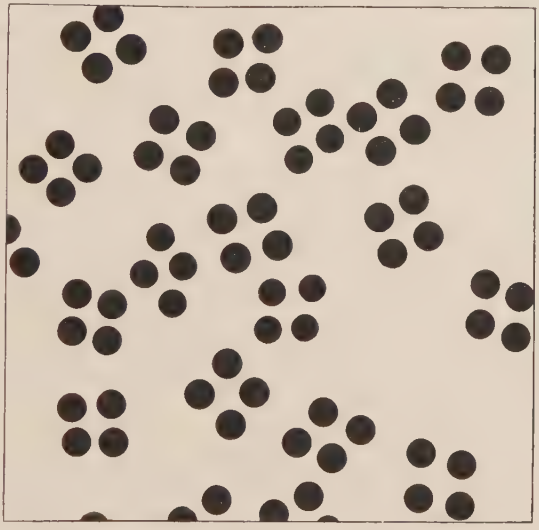


FIG. 117.—*Stropharia semiglobata*. A dark area of the hymenium with only the spores represented, to show the density of distribution of the basidia of the present generation. The basidia bearing spores are only one-sixth to one-seventh of the whole number. Each side of the square = 0·15 mm. Drawn with the *camera lucida*. Magnification, 440.

(5) *paraphyses*, *e e*, numerous non-protuberant rounded or oval elements, more or less hidden by the enlarged tops of the basidia, never bearing sterigmata or spores, and becoming larger and more and more emptied of their protoplasmic contents with the gradual exhaustion of the hymenium; and (6) *pleurocystidia*, *f*, elements

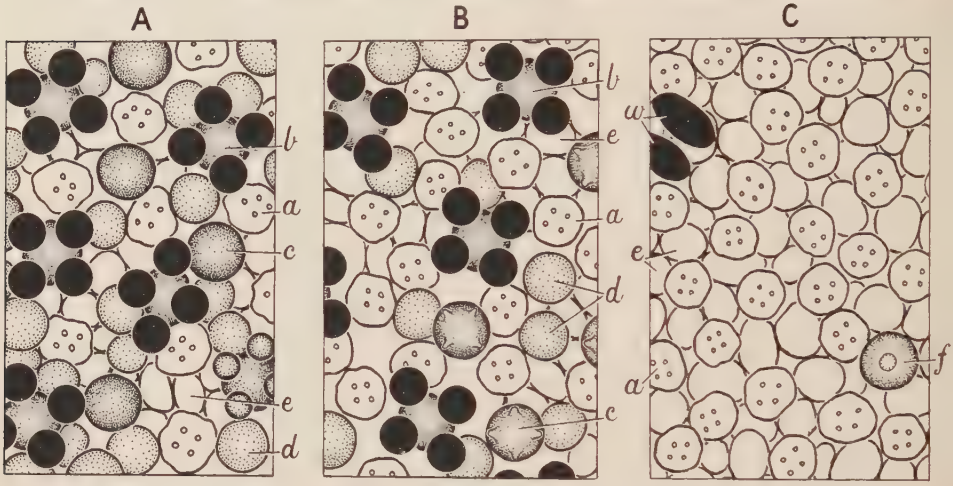


FIG. 118.—*Stropharia semiglobata*. Surface view of the hymenium: A, one day after the opening of the pileus and beginning of spore-discharge; B, two days after; and C, about eight days after, when spore-discharge has ceased. *a*, a past-generation basidium (with four sterigmatic stumps); *b*, a present-generation basidium (bearing spores); *c*, a coming-generation basidium (heavily shaded with dots); *d*, a future-generation basidium (lightly shaded with dots); *e*, a paraphysis (unshaded); *w*, waste spores adhering to the hymenium; *f*, a cystidium. In A and B respectively the number of elements on the equal areas is as follows: past-generation basidia, 10 and 20; present-generation basidia, 6 and 6; coming-generation basidia, 5 and 4; future-generation basidia, 23 and 10; paraphyses, about equal numbers. In C, all the basidia now belong to past generations, and the paraphyses have become larger and can therefore be more clearly distinguished. In A and B, only those paraphyses are drawn which could be clearly distinguished, the rest are omitted. Magnification, 580.

occurring singly (one shown in C), few in number, scattered irregularly throughout the hymenium, with dense persistent contents, differing from the basidia in never producing sterigmata and spores and from both basidia and paraphyses by ending in a protuberant peg-like point. Pleurocystidia, *i.e.* cystidia which are situated on the sides of the gills, do not occur in *Panaeolus campanulatus*, so that, in possessing these elements in this situation, *Stropharia semiglobata* differs from that fungus and comes to have six classes of hymenial elements instead of only five.

The gradual exhaustion of the hymenium, as shown in Fig. 118, may be realised at a glance by noting the gradual increase of the past-generation basidia as one passes from A to C. Corresponding with this increase is a decrease in the number of future-generation basidia. The number of present-generation and coming-generation basidia is about the same for A and B. This accords with other observations which have taught me that, in *Stropharia semiglobata*, during the first few days of the spore-discharge period, on any given area of the hymenium, the number of basidia producing spores at any one time remains fairly constant, and that, as in *Panaeolus campanulatus*, during the last few days of the spore-discharge

The Number of Elements in the Hymenium of Stropharia semiglobata.

Nature of Elements.		Age of Fruit-body after Commencement of Spore-discharge.		
		Area A : one day.	Area B : two days.	Area C : six days.
Generations of Basidia.	Past	10	20	32
	Present	6	6	0
	Coming	5	4	0
	Future	23	10	0
Paraphyses		$20 + x$ (= 24?)	$20 + y$ (= 24?)	44

period when the activity of the hymenium is approaching its close, there is a tendency for this number to decrease. In the area A there are present about 44 basidia. Let us assume that the average number of basidia which successively bring their spores to maturity on this area is 5. Then, by division, we can calculate that, altogether, such an area as A would give rise to 9 successive generations of basidia. If, however, we assume what may well be nearer the truth, namely, that the average number of basidia of each generation is 4 instead of 5, then the number of successive generations on the area A would be increased to 11. The size of the paraphyses gradually increases with the progressive collapse of more and more basidia. This fact may be verified by comparing the few paraphyses clearly outlined in the area A with the paraphyses shown in the area C.

In the above Table the nature and number of the elements in all three of the areas shown in Fig. 118 are set forth. Parts

of elements have been counted as wholes. The letters x and y in connection with the paraphyses indicate paraphyses of uncertain number which were not clearly perceived owing to optical difficulties. However, a comparison of the areas A and B with the area C suggests that x and y are each equal to about 24.

The paraphyses, *i.e.* the permanently sterile elements, are just as distinct in the hymenium of *Stropharia semiglobata* as in that of *Panaeolus campanulatus*. They can be most easily distinguished in a piece of exhausted hymenium such as that shown in Fig. 119. Here the tops of the contracted basidia *b* somewhat overlie the paraphyses *p*. A pleurocystidium is shown at *c*, and waste spores at *w*. A more complete analysis of the exhausted hymenium is given in Fig. 120, where the basidia and paraphyses (from different areas) have been drawn separately. At A there are shown the basidia without the paraphyses, and at B the paraphyses without the basidia. The drawing C is similar to B except for the fact that it includes four pleurocystidia, whereas none of these elements are present in B. By comparing A with B and C, which all represent equal areas of the hymenium, one may observe that the paraphyses are somewhat more numerous than the basidia and, further, that the paraphyses tend to be connected into chains so that they avoid isolation. On the other hand, individual basidia often stand apart from their neighbours, from which they are separated by paraphyses.

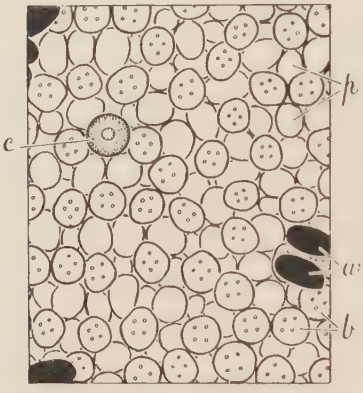


FIG. 119.—*Stropharia semiglobata*. Exhausted hymenium in surface view. *b*, collapsed basidia, each with four sterigmatic stumps; *p*, paraphyses; *c*, a cystidium; *w*, waste or undischarged spores. Magnification, 440.

Two transverse sections through the hymenium and subhymenium of *Stropharia semiglobata* are represented in Fig. 121. The upper one, A, shows the hymenium in the early part of the spore-discharge period, *i.e.* at a stage about equivalent to that indicated in the surface view represented in Fig. 118, A; while the

lower one, B, shows the hymenium in the exhausted condition at the end of the spore-discharge period, *i.e.* at a stage corresponding to that indicated in Fig. 118, C. In the upper drawing we can discern that the hymenium is made up of past-generations basidia (*a*), present-generation basidia (*b*), coming-generation basidia (*c*), future-generations basidia (*d*), small sterile paraphyses (*e*), and cystidia (*f*). The cystidium is club-shaped and has a slender stalk

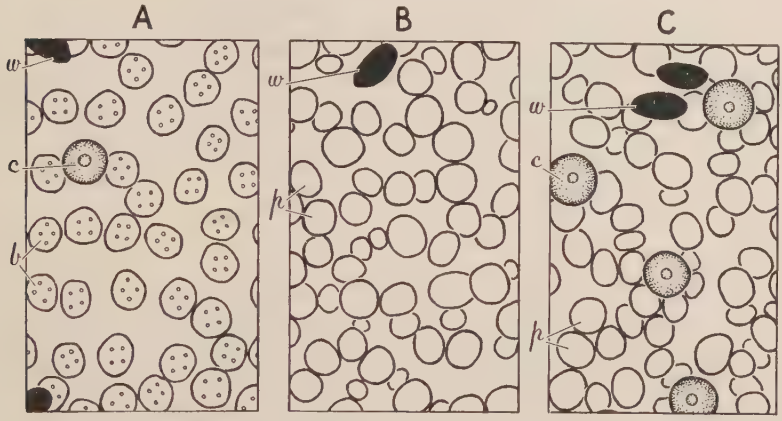


FIG. 120.—*Stropharia semiglobata.* Sketches of portions of an exhausted hymenium after spore-discharge has ceased. A shows: the collapsed basidia, *b*, each with four sterigmatic stumps; a cystidium, *c*; and parts of two waste spores, *w*. The paraphyses are omitted. B shows paraphyses, *p*, and one waste spore, *w*, only. The basidia are omitted and no cystidia are present. C shows: paraphyses, *p*; four cystidia, *c*; and two waste spores, *w*. Magnification, 440.

which springs from one of the lowest cells of the subhymenium. The present-generation basidium farthest to the left has just discharged its first spore and is about to discharge its second. As a preliminary to the second discharge a drop of water has been excreted at the spore-hilum. The drop has developed within the last five seconds and has almost attained its maximum size. In the lower drawing it will be seen that the exhausted hymenium is made up of collapsed past-generations basidia (*a*), swollen paraphyses (*e*), and cystidia (*f*). The large cell, *g*, is an aborted basidium. It contained thick protoplasm on its walls and a large central vacuole, and it seems to have become swollen instead of producing spores.

That the basidia in any small area of the hymenium come to

maturity in a series of successive generations was proved not merely by inference from such studies as have been recorded in the drawings of Fig. 118, but also by direct observation. A fruit-body, which had not long expanded its pileus and was in the earliest phase of its

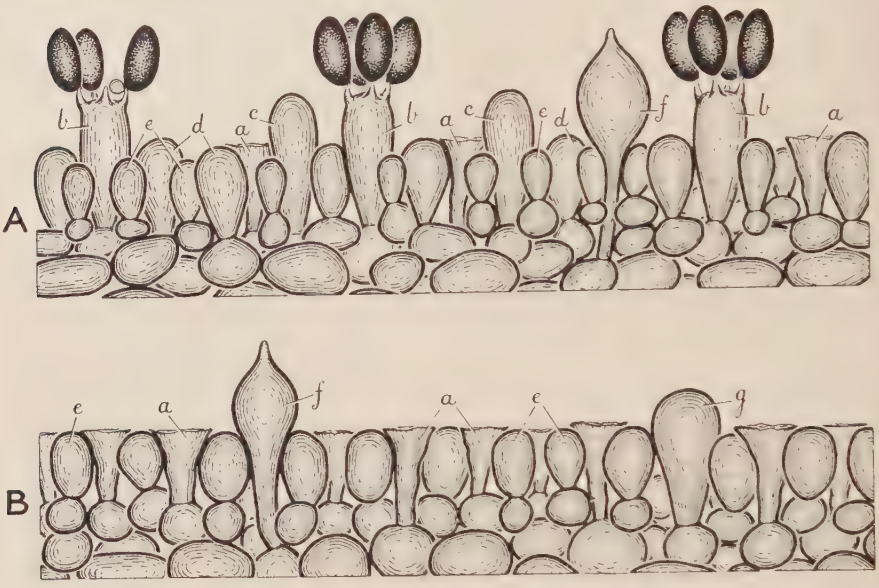


FIG. 121.—*Stropharia semiglobata*. Transverse sections through a gill showing the hymenium and subhymenium. A, about a day after the beginning of spore-discharge; *a a*, past-generation basidia; *b b*, present-generation basidia; *c c*, coming-generation basidia; *e e*, paraphyses; *f*, a cystidium; the present-generation basidium farthest to the left has just discharged one spore and is about to discharge another spore the hilum of which has just excreted a water-drop. B, from an exhausted gill at the end of the spore-discharge period; *a a*, past-generation basidia; *e e*, paraphyses; *f*, a cystidium; *g*, an aborted basidium which has become much swollen, but which has not produced any spores. Magnification, 588.

spore-discharge period, was obtained from a pasture. Straightway one of its gills was dissected off the pileus and placed flat in a compressor cell, and a little water was made to pass between the lower hymenial surface and the glass base of the apparatus. Another drop of water of small size was then placed on the glass base in a position where it could not touch the gill, and the preparation was completed by capping the compressor cell with its lid. On examining the preparation with the low power of the microscope, it was found that the upper hymenium of the gill afforded an admirable

object for study. There was a minute crack in the cover-glass, and it was found necessary to renew the water in the cell once during the investigation. A small portion of a dark area, from which the spores were being discharged, was chosen for special study ; and in the course of eight hours' continuous watching by myself and by my nephew, Mr. Bernard Workman, to whom I am much indebted for timely assistance, I succeeded in observing the following : (1) the last phase of one generation of basidia, including the discharge of the spores and the collapse of the basidium-bodies ; (2) the development and discharge of the spores of a second generation of basidia, followed by the collapse of the basidium-bodies ; and (3) the development of spores on the sterigmata of a third generation of basidia. The horizontal-microscope method, which was employed in a similar investigation for *Panaeolus campanulatus*,[1] has various advantages over the just-described vertical-microscope method, for it permits one to observe a gill which is attached to a fruit-body in such a way that the spores discharged from it are shot clear of the hymenium, and it permits of the observations being carried on for several days instead of for a portion of one. Nevertheless, the vertical-microscope method employed in the present investigation sufficed me to attain the end in view. Its disadvantages are that the gill has to be removed from the fruit-body and therefore will not continue to develop normally for many hours, and also that the spores which are shot upwards must necessarily fall back again on to the hymenium where their accumulation tends to hinder one from seeing the hymenial elements clearly. Its chief advantage lies in its simplicity, the only apparatus involved being an ordinary microscope and a compressor cell.

The developmental waves, which have already been described as passing through the hymenium, were actually observed in their progress. In the centre of the field of the microscope was an area which was at first dark, and waves of development travelled out from it radially, somewhat in the way represented in Fig. 116 (p. 332). The passage of a single undulation across the field of the microscope occupied several hours.

Close attention to the small area specially chosen for minute

[1] Chap. X, pp. 260–264.

study revealed the following facts. The sterigmata of the coming-generation basidia begin to develop a short time (30 minutes ?) before the immediately adjacent present-generation basidia shoot away their spores (*cf.* Fig. 118, B, *c*, p. 334). Spores begin to develop on the sterigmata of a second-generation basidium about twenty minutes after the spores of an adjacent first-generation basidium have been shot away. The spores are rather slow in developing from their first rudiments to full size, for an hour and ten minutes are occupied in the process. Pigmentation of the spore-walls begins about one hour after the spores have attained full size, and continues for about two hours and a half. The spores remain on their sterigmata about one hour after they have become fully pigmented and, invariably, their violent discharge is preceded by the excretion of a drop of water at the hilum. Waste spores accumulate on the hymenium as a result of over-excretion of the water-drop, in the same manner as was described for *Panaeolus campanulatus*. The time occupied by the development and discharge of the spores of the second-generation basidia observed, from the moment when the spores of adjacent first-generation basidia were discharged, was about six hours.

The chief facts observed in connection with the second-generation basidia under observation may be set out as follows. The times represent the average for six basidia. The zero of the time-scale is the moment of the first appearance of spore-rudiments on the tops of the sterigmata.

Development of the Spores of a Single Generation of Basidia in Stropharia semiglobata.

Observations.	Hours.	Minutes.
First appearance of spore-rudiments on the sterigmata	0	0
Spores have grown to full size	1	10
The spore-walls begin to exhibit pigmentation	2	10
The spore-walls are fully pigmented	4	40
The first of the four spores is discharged	5	40
The spores on basidia of the succeeding generation begin to develop	6	0

I suspect that the later generations of basidia, as in *Panaeolus campanulatus*, take increasingly longer periods to develop and

discharge their spores. Possibly the six hours actually observed for one of the earliest of the basidial generations may be lengthened out to seven or eight for the later generations.

Rate of Discharge of the Spores of a Basidium and Collapse of the Basidium-body.—The following observations were made with the horizontal microscope in the manner fully described for *Panaeolus campanulatus* (Fig. 91, p. 261). The gill attached to the pileus was developing normally.

For several basidia the times of discharge for the four spores were carefully observed. I called each observation and my laboratory attendant, Mr. S. G. Churchward, kindly recorded the time in seconds. The four spores of any one basidium were always discharged in succession in the course of about two to ten minutes. If we make the zero of the time-scale the moment at which the first of the four spores is shot away, then the times for the discharge of all four spores for three basidia which were observed may be set out as follows.

The Discharge of the Four Spores of a Single Basidium in Stropharia semiglobata.

	Basidium I.		Basidium II.		Basidium III.	
	Time of Discharge.		Time of Discharge.		Time of Discharge.	
	Minutes.	Seconds.	Minutes.	Seconds.	Minutes.	Seconds.
First spore	0	0	0	0	0	0
Second spore	4	48	0	53	1	32
Third spore	5	33	5	48	1	37
Fourth spore . . .	5	53	7	15	1	55

One may conclude from these observations that the intervals between the discharge of the first and second, of the second and third, and of the third and fourth spores, are by no means constant but highly variable, ranging between nearly five minutes and only five seconds. It is not unlikely that very rarely two spores are shot off from the same basidium at practically the same instant; but successive discharge is evidently the rule. The average length of time taken for the discharge of all the spores from each of three basidia was five minutes and one second.

During the time that a basidium is discharging its spores, the basidium-body and the sterigmata do not appear to undergo any alteration. The basidium-body, before, during, and immediately after spore-discharge, owing to the convexity of its top, appears light in the centre and dark at the periphery. I watched several basidia shed all their spores, and continued to watch them for some time after the last spore of each had disappeared, in order to become acquainted with the phenomenon of their collapse. It was found that, until about twenty minutes after the last spore has been shot away, a basidium remains prominent and apparently unaltered, but that at the end of this time it undergoes a rapid change. In the course of about one more minute, its sterigmata are drawn together and the end of the basidium-body becomes darkened and relatively difficult to observe. There can be no doubt that during this minute the basidium collapses: the end of the basidium-body becomes concave, the sterigmata are drawn down into the concavity so formed, and at the same time the basidium sinks so that its end is no longer protuberant beyond the general level of the hymenium marked by the exterior of the paraphyses. For four different basidia the actual moment at which the process of collapse began after the discharge of the last spore was observed to be 23, 16, 16, and 20 minutes respectively, or, upon the average, about 19 minutes.

The actual moment of the collapse of the basidia of any one generation precedes only by a few minutes the beginning of the development of the spores on the sterigmata of the basidia of the succeeding generation. If, owing to any miscarriage of development, the spores of a basidium do not happen to be discharged when they should be under normal conditions, the basidium collapses apparently at the normal time, *i.e.* at the time at which it would have collapsed if it had discharged its spores. It is obvious, therefore, that basidial collapse takes place just sufficiently soon to secure that any undischarged spores of one generation shall be dragged down to the general level of the hymenium before the already protuberant basidia of the succeeding generation begin to develop their spores. The undischarged spores of one generation are moved by basidial collapse from their place of origin to their

place of rest in so timely a manner that they are unable even to touch, much less adhere to and interfere with, the spores of the basidia of the next generation. This protection of the newly-developing spores from the mechanical contact of old undischarged spores is one of those fine points in the organisation of the hymenium which only a very detailed investigation could possibly reveal. In concluding the discussion of this subject, it may be remarked that, since a basidium collapses very shortly after discharging its last spore, it is clear that it produces one set of spores and one only.

The Spore-fall Period.—Spore-deposits were collected during successive days beneath the pileus of a fruit-body grown on horse dung under a bell-jar in the laboratory. The fruit-body had just opened when the observations were begun. A certain number of spores was shed during the first day, but the most copious deposits were collected during the second and third days. The spore-deposit made during the fourth day was relatively poor. During the fifth and sixth succeeding days, spores continued to be liberated but in ever diminishing numbers until, on the seventh day, spore-discharge ceased and the fruit-body collapsed. During the last stages of hymenial activity, the gills lost their mottled appearance and took on a uniform dirty-yellow colour. We may conclude, therefore, that spore-discharge from a fruit-body may continue for about six days but that it is most active during the first three days.

Wasted Spores.—Spores which fail to be properly discharged become attached to the hymenium of *Stropharia semiglobata* in the manner already described for *Panaeolus campanulatus*, but, at least occasionally, in somewhat greater numbers than for the latter fungus.

A fruit-body, which had been grown on horse dung under a bell-jar in the laboratory, was examined as soon as it had ceased to shed spores. All the wasted spores on an area of the hymenium 0·5 mm. long and 0·33 mm. wide were sketched with the *camera lucida* as shown in Fig. 122. The cystidia *k k* were drawn in a similar manner. The exhausted basidia and the paraphyses were put into the drawing semi-diagrammatically by knitting together various exact *camera-lucida* sketches similar to that shown in

Fig. 119 (p. 336). The resulting Fig. 122 forms a basis for calculating the percentage of wasted spores. It was found by counting that, on the area of the hymenium under discussion, there were 231 wasted spores. But the area contains 2,896 sterigmatic stumps. Since each sterigma must have given rise to a spore, the total number of spores produced by the area must have been about 2,896. From these figures it may be calculated that the wasted spores were just under 8 per cent. of the whole number produced. Some areas of the hymenium, as large as the one investigated, were observed to be much more free from wasted spores, and others less free. Probably, for the whole fruit-body, the percentage of wasted spores was between 7 and 8.

Possibly, in nature, the number of spores which are wasted because they are not properly liberated is less than that obtained in my investigation in the laboratory. Under a bell-jar the air surrounding a fruit-body grown on moist horse dung tends, especially at night, to become saturated with moisture ; and it is not unlikely that inhibited transpiration is prejudicial to the discharge of spores. It may be that the water-drop defect,[1] which was fully dealt with in connection with *Panaeolus campanulatus*, becomes augmented under these conditions, with a consequent decrease in the number of spores set free. Investigations upon the number of spores wasted by fruit-bodies of *Stropharia semiglobata* under natural conditions, however, have not been undertaken.

The wasted spores are by no means uniform in appearance. Thus in Fig. 122, while most of the spores are pigmented, thirty-two of them, as indicated by the shading, have walls which are either colourless or only partially coloured. There are several heaps of four spores, each heap representing the product of a single basidium. The heaps shown at *a*, *b*, *c*, *d*, *e*, *f*, *g*, *h*, and *i*, consist of immature spores, and those shown at *j* and *l* of mature spores. Some of the spores, *e.g.* those at *l*, are under-sized, whilst others, *e.g.* three in the middle of the Figure at the top, are much larger than the average. Here, as in other species of Hymenomycetes, one often finds monstrous spores among those which are wasted. From data derived from Fig. 122, one may calculate that the number

[1] Fig. 104, p. 308.

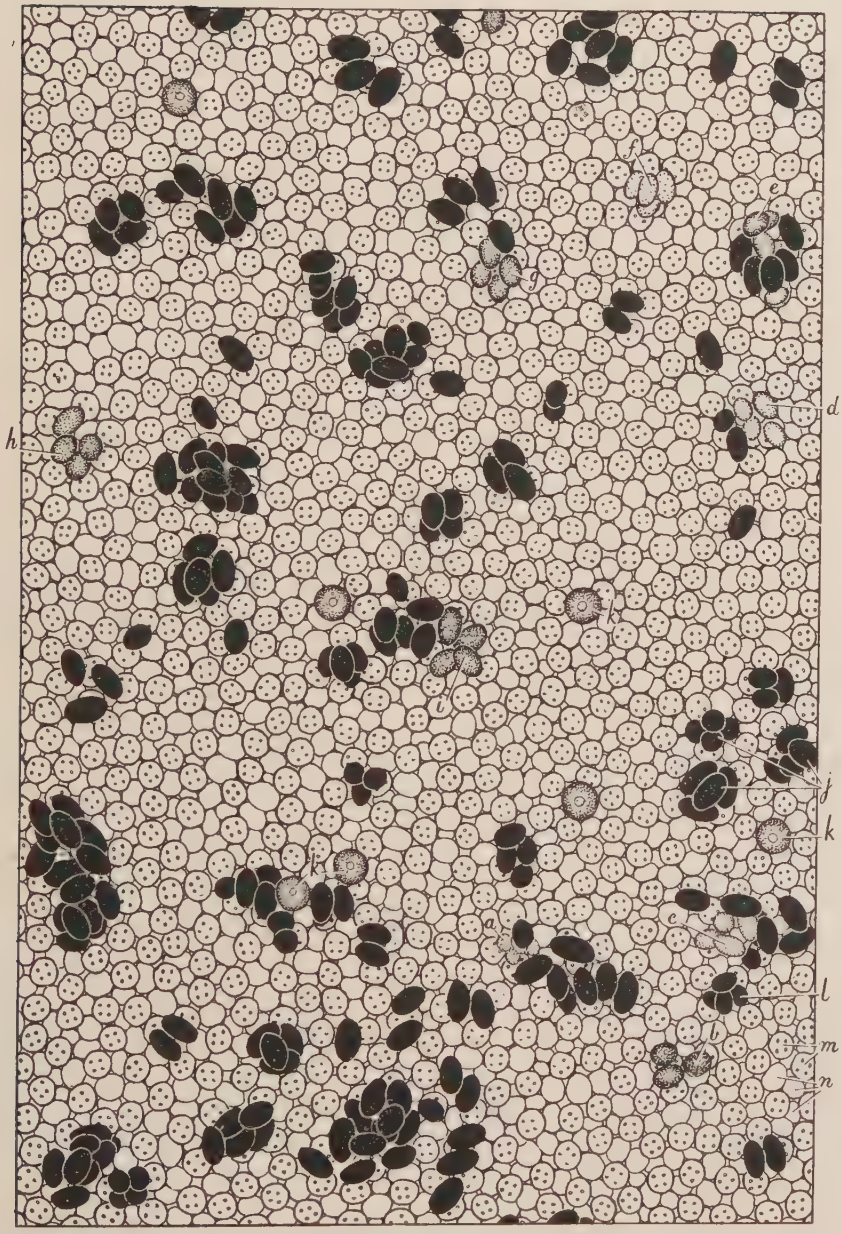


FIG. 122.—*Stropharia semiglobata.* An area of the hymenium 0·5 mm. long and 0·33 mm. wide, drawn after spore-discharge had ceased, showing the exact number and arrangement of the spores which were left adhering to the hymenium. The spores shown in black were fully pigmented, those shaded heavily with dots partially pigmented, and those shaded lightly with dots colourless. The hymenium is made up of: exhausted basidia, *m*, each with four sterigmatic stumps; paraphyses, *n*; and seven cystidia, *k*, irregularly scattered. There are several heaps of four spores, each heap representing the product of a single basidium: *a*, *b*, *c*, *d*, *e*, *f*, *g*, *h*, *i*, groups of immature spores; *j* and *l*, groups of fully pigmented spores. The waste spores form just under 8 per cent. of all the spores which were produced on the whole area. Magnification, 323.

of spores produced on one square millimetre of the hymenial surface of *Stropharia semiglobata* is about 9,000 and that of these, under laboratory conditions, some 720 may be wasted. When the figures are set forth in this way, one perceives that, notwithstanding the number of wasted spores, the efficiency of the fruit-body as a whole for the production and liberation of spores still remains very high.

In concluding this Chapter, it may be stated that there is no essential difference in the structure of the hymenium of *Stropharia semiglobata* and of *Panaeolus campanulatus*. Both are built on the same plan and function in the same manner. The fruit-bodies of both species provide us with excellent examples of the Panaeolus Sub-type of organisation.

CHAPTER XII

ANELLARIA SEPARATA

General Remarks—The Production and Liberation of Spores—A Photograph of the Hymenium

General Remarks.—*Anellaria separata,* like *Panaeolus campanulatus* and *Stropharia semiglobata,* is one of the best known of coprophilous fungi. It commonly occurs in England on horse dung or cow dung in pastures in the manner shown in Fig. 123, and I have also found it coming up spontaneously on horse dung brought into my laboratory from the streets of Winnipeg in winter.

Some cow dung, obtained in South Wales, was dried by Miss E. M. Wakefield and sent to me at Winnipeg. Four months after being dried, it was moistened and placed in a damp chamber. After this, in the course of a few weeks, it gave rise to fruit-bodies of *Anellaria separata* (Fig. 125), from which fact we may draw the conclusion that the mycelium can retain its vitality in the desiccated condition for a period of at least four months. In nature, during dry spells of weather in summer, it not infrequently happens that dung-masses are baked to dryness by the sun's heat. It is evident, from the observations just described, that such drying does not necessarily impair the vitality of the mycelium of *Anellaria separata* with which the dung may be infected; and, doubtless, in dried dung in fields, the mycelium often remains at rest for many days or even weeks until rain comes again. Then the mycelium resumes its growth and may give rise to fruit-bodies. The exact state which the mycelium assumes when becoming quiescent, however, requires further investigation.

There is no difficulty in cultivating the fungus from spores in the laboratory. Some horse dung was sterilised and then infected with the spores of a fruit-body which had come up spontaneously

FIG. 123.—*Anellaria separata*, a coprophilous agaric, coming up on horse dung. All the fruit-bodies which come to perfection arise in dark crevices underneath or between the dung-balls. This is probably due to the fact that, as in *Coprinus stercoreus*, strong light inhibits the development of small fruit-body rudiments. The pileï are forced upwards between the dung-balls or through individual dung-balls by the pressure of the negatively geotropic stipes. Photographed by R. Hancock at Sutton

on cow dung. On the twenty-ninth day after the spores had been sown, the first fruit-body began to shed its spores. It is thus proved that the fungus can pass through the whole of its life-history, from spore to spore, in the course of a single month.

The following is a brief description of the fruit-body, which differs but little from that given by Massee.[1] Pileus 2·5 to 3·3 cm. high (varying up to 5·5 cm., *vide* Fig. 124), 2·5 to 4·25 cm. broad (varying up to 6 cm., *vide* Fig. 124), ovate, then campanulate, not expanding, viscid, even, ochraceous, then whitish, shining, flesh rather thick ; gills adfixed, ascending, thin, crowded, broad, mottled greyish-black, margin paler ; stipe 8 to 16 cm. long, straight, base sub-clavate, attenuated upwards, whitish, shining, apex striatulate, ring persistent, distant ; spores black, opaque, 19–21 μ long, 10–11 μ broad, and 9 μ wide.

Massee states that the fruit-bodies are from 3 to 5 inches long. However, I have gathered specimens 6 inches long, and according to Stevenson [2] the maximum length is about 8 inches. Sometimes the pileus is very large and the stipe relatively short, as is shown in Fig. 124. Dr. Somerville Hastings has informed me that in the Alps of Switzerland, at a height of from 6,000 to 7,000 feet, the pilei of *Anellaria separata* are well-developed, but the length of the stipe is not more than twice the breadth of the pileus.[3] It is evident that the length of the stipe of *A. separata* varies greatly in response to external conditions.

The spores have three different dimensions : length, breadth, and thickness. The difference between the breadth and thickness may best be perceived by looking down on the spores, so that one obtains an endwise view of them like that shown in Fig. 128. Other authors have taken notice of the length and breadth only. Massee [4] states that the spores measure 10 by 7 μ. My average measurements for length and breadth are 20 and 10·5 μ respectively, so that the spores of my specimens were twice as long as those of

[1] G. Massee, *British Fungus-Flora*, London, 1892, vol. i, pp. 330–331.

[2] J. Stevenson, *Hymenomycetes Britannici*, Edinburgh and London, vol. i, 1886, p. 338.

[3] For a photograph of the Alpine form of *Anellaria separata vide* these *Researches*, vol. iii.

[4] G. Massee, *loc. cit.*

Massee, and as broad as his were long. Keith's[1] measurements

Fig. 124.—*Anellaria separata*, on horse dung. A fruit-body with a very large pileus and a relatively short and thick stipe. The pileus (clay-whitish in colour) is smooth, and cracked in a characteristic manner. The annulus is unusually near the base of the stipe. Photographed at Scarborough, England, by A. E. Peck. Natural size.

were 16–22 by 11–12 μ and Cotton's[2] 18–22 by 10–12 μ, *i.e.*

[1] Keith, in Stevenson's *Hymenomycetes*, *loc. cit.*

[2] A. D. Cotton, private communication.

substantially the same as my own. It seems to me, therefore, that Massee's measurements do not represent the average for the species and that he either examined a fruit-body with unusually small spores or, by inadvertence, allowed some error to creep into his record of the figures obtained.

The annulus upon the stipe is a structure which exhibits considerable variation. In nature, it is sometimes relatively much expanded and at other times relatively inconspicuous, although it is never absent. It is usually composed of a continuous membrane which takes the shape of an inverted cup (*cf.* Figs. 125 and 127). Under cultivation, the annulus is still more variable. In some of the fruit-bodies reared in the laboratory, the annulus was prefectly normal, while in others it became divided into long strings passing from the stipe to the periphery of the pileus and thus coming in a measure to resemble the cortina in the genus Cortinarius (Fig. 126). In yet other specimens no annulus was left attached to the stipe but instead there was a broad band of sterile tissue attached to the edge of the campanulate pileus. Some of the specimens, if considered by themselves, would have been more fitly included in the ringless genus Panaeolus than in Anellaria. These observations seem to me to show that, after all, the ring in Anellaria is not a very

FIG. 125.—*Anellaria separata.* A fruit-body grown on horse dung in confinement under a bell-jar. The annulus, covered with spores at the top, is abnormally large. The black spore-deposit on the top of the pileus was formed owing to convection currents carrying spores upwards after their discharge from the gills. Natural size.

Fig. 126.—*Anellaria separata.* A fruit-body which came up spontaneously on horse dung in a moist chamber at Winnipeg. The abnormal veil is arachnoid like the cortina of Cortinarius. Natural size.

deep-set character. The species of Panaeolus and of Anellaria are so nearly alike, except for the ring, that Fries never separated them. The genus Anellaria was subsequently constructed by Karsten[1] to include the ringed Panaeoli. While this distinction, doubtless, is of some convenience to field-workers, I cannot help feeling that, from the standpoint of relationship, the view of Fries is the more correct one. The gap between Panaeolus and Anellaria appears to me to be very slight indeed, when compared with the gap between Panaeolus and other genera of Melanosporae, namely, Coprinus and Psathyrella.

The Production and Liberation of Spores.—The organisation of the fruit-body for the production and liberation of spores was found to be the same in all essentials as in *Panaeolus campanulatus*. The fungus clearly belongs to the Panaeolus Sub-type of the Aequi-hymeniiferae. As a member of the Aequi-hymeniiferae, its gills are wedge-shaped in vertical section and positively geotropic, so that every part of the hymenium in a normally oriented fruit-body comes to look more or less downwards. Moreover, every part of its hymenium (every square mm.) successfully produces and liberates spores during the whole period of spore-discharge. As a member of the Panaeolus Sub-type, its gills are mottled (Fig. 127, D and E). The mottling of its

[1] P. A. Karsten, *Rysslands, Finlands och den Skandinaviska Halföns Hattsvampar,* Helsingfors, 1879, p. 517.

gills is strongly marked and just as distinct as in *Panaeolus campanulatus* and *Stropharia semiglobata*.

The organisation of the hymenium of *Anellaria separata* was found to be similar to that of *Panaeolus campanulatus*, so that it is unnecessary to describe it or to illustrate it in all its details. Among the facts yielded by a study of the living gills were the following. On each area of the hymenium the basidia come to maturity in a series of successive generations. Coming-generation basidia on any hymenial area do not develop their spores until the spores of the present generation have been shed. The time elapsing between the discharge of the spores of two successive generations of basidia on the same small hymenial area amounts to several hours. With the horizontal microscope, a single hymenial area of a gill which had been shedding spores for about 24 hours was watched in the manner already described,[1] and it was found that from 10·5 to 11 hours elapsed between the spore-discharge of two successive generations of basidia. Unfortunately, the fruit-body observed was not quite normal in its activities, as the proportion of its undischarged to its discharged spores was unusually large. However, notwithstanding the accumulation of wasted spores upon the hymenium, it became sufficiently obvious that the rate of development of each generation of basidia was of the same order as for *Panaeolus campanulatus*. Paraphyses are present in the hymenium, and they remain living until spore-discharge ceases and the fruit-body collapses. During the gradual exhaustion of the hymenium they grow in size. The shape and distribution of the paraphyses and basidia are similar to those of *Panaeolus campanulatus*. From the latter fungus *Anellaria separata* differs in possessing pleurocystidia. These, like those of *Stropharia semiglobata*, are few in number and scattered at relatively great intervals among the paraphyses and basidia. Each is more or less clavate and terminates in a nipple-like ending which projects slightly above the hymenium. The white margin of a gill, like that of *Panaeolus campanulatus* or *Stropharia semiglobata*, is clothed with hair-like cheilocystidia.

The collapse of the basidia after they have discharged their spores was studied in more detail than in *Panaeolus campanulatus*.

[1] Figs. 91 and 92, pp. 261 and 263.

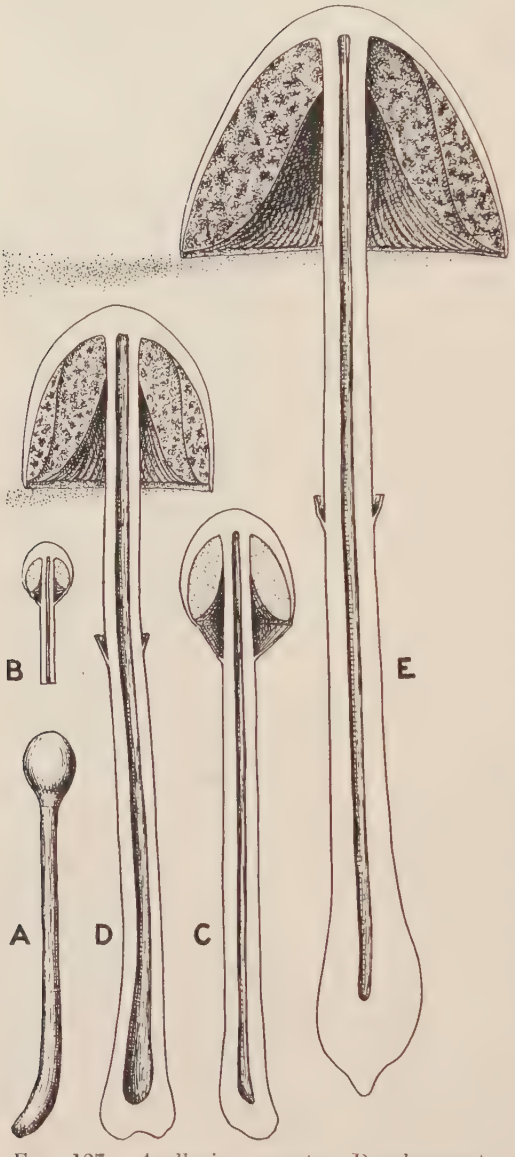


FIG. 127.—*Anellaria separata*. Development of adnate gills. A, very young fruit-body of which B is a section. C, D, and E, other stages in succession. The long axes of the gills do not undergo a large movement just before spore-discharge begins. The mottling of the gills and the discharge of a stream of spores are also shown in D and E. Natural size.

The observations were made with the horizontal microscope in the manner shown in Fig. 92 (p. 263). First, the length of time required for the discharge of all the four spores of a single basidium, counting from the discharge of the first spore, was noted. As a rule, it was found to be about five minutes, as in *Stropharia semiglobata*. Taking the time of discharge of the first spore as zero, the times for the discharge of the other three spores in one particular basidium were as given in the Table on the opposite page.

At the moment when a basidium discharged its last spore, the time was noted. The basidium-body with its four sterigmata could still be seen projecting from the hymenium. For some fifteen to twenty minutes the turgidity of the basidium-body appeared to be unimpaired, but at the end of this time collapse took place in a few seconds. The four sterigmata fell inwards

toward the basidium-axis, the basidium-body shortened and its end changed from a convex to a concave shape. As the concavity was being produced, the basidium-body changed from a bright appearance to a uniform grey. Within a few seconds after the beginning of the collapse, the whole basidium came to resemble other collapsed basidia and could not be distinguished from them.

The Discharge of the Four Spores of a Single Basidium in Anellaria separata.

	Spores.			
	First.	Second.	Third.	Fourth.
Moment of discharge .	0	3 minutes, 30 seconds	3 minutes, 47 seconds	5 minutes, 20 seconds

Altogether the time of collapse of four basidia was carefully noted, the zero of the time-scale being in each case the moment of discharge of the last of the four spores :

The first basidium observed collapsed after 22 minutes,
,, second ,, ,, ,, ,, 15 ,,
,, third ,, ,, ,, ,, 20 ,,
,, fourth ,, ,, ,, ,, 21 ,,
The average time of collapse was . . 19·5 ,,

We may say, therefore, that in *Anellaria separata* the collapse of a basidium usually takes place about twenty minutes after the discharge of the last of its four spores. This interval of time is about the same as that which was observed for *Stropharia semiglobata*.

Among the abnormalities of the basidia the following were noted. Occasionally, a basidium was observed to bear five spores instead of the usual four. Occasionally, a basidium was seen with one aborted spore and the other three of the usual size or possibly a little larger. The aborted spore was only about one-third of the usual diameter and therefore relatively very small in volume.

A Photograph of the Hymenium. — When studying the hymenium of *Panaeolus campanulatus*, I endeavoured to photograph the living hymenium but, unfortunately, the results were

not clear enough for publication. However, with *Anellaria separata*, owing to improvement in my methods, I have had more success. In Fig. 128 is shown a photograph of the spores belonging to the present spore-bearing generation of basidia on one of the dark areas of the hymenium. One can see that the photograph resembles part of the drawing which was given for the hymenium of *Panaeolus campanulatus* in Fig. 89 (p. 257). The four black spores of each basidium can be clearly made out, and one can see that adjacent spore-bearing basidia are separated by such spaces that their spores cannot touch one another during development and discharge. Evidently the basidia of the present generation are all of about the same age, for their spores are highly pigmented and basidia with half-grown or colourless spores are entirely absent from the area. Another point demonstrated by the photograph is that the spore-bearing basidia are monomorphic, *i.e.* all protrude to about the same distance above the general level of the hymenium, for only on this supposition can one account for the fact that the spores are all in focus in a single plane. The reader may be reminded here that basidial monomorphism is one of the characteristics of the Panaeolus Sub-type. The tendency of the four spores of a basidium to be arranged in a rhomboidal manner, where a basidium is rather nearer than usual to its neighbours, is well shown just to the right of the middle of the Figure. The meaning of the arrangement is the same as that already explained in connection with *Panaeolus campanulatus*.[1] A basidium at the bottom of the Figure, in the middle line, has already lost one of its spores and now only possesses three. All the spores are in view endwise on. Seen thus, they are not round but oval in outline. This confirms the statement, made on a previous page, that every spore of *Anellaria separata* has three differing dimensions : length, breadth, and thickness. In the middle of each group of four spores can be seen a light rounded spot. This is produced by the convex top of the basidium-body, which in concentrating the light-rays has a lens-like effect. Here and there between the groups of spores can be seen similar spots. These correspond to the convex ends of the bodies of basidia of the coming generation.

[1] Pp. 322–324.

The photograph reproduced in Fig. 128, so far as I know, is the first ever published which exhibits hymenial structure.[1] I shall

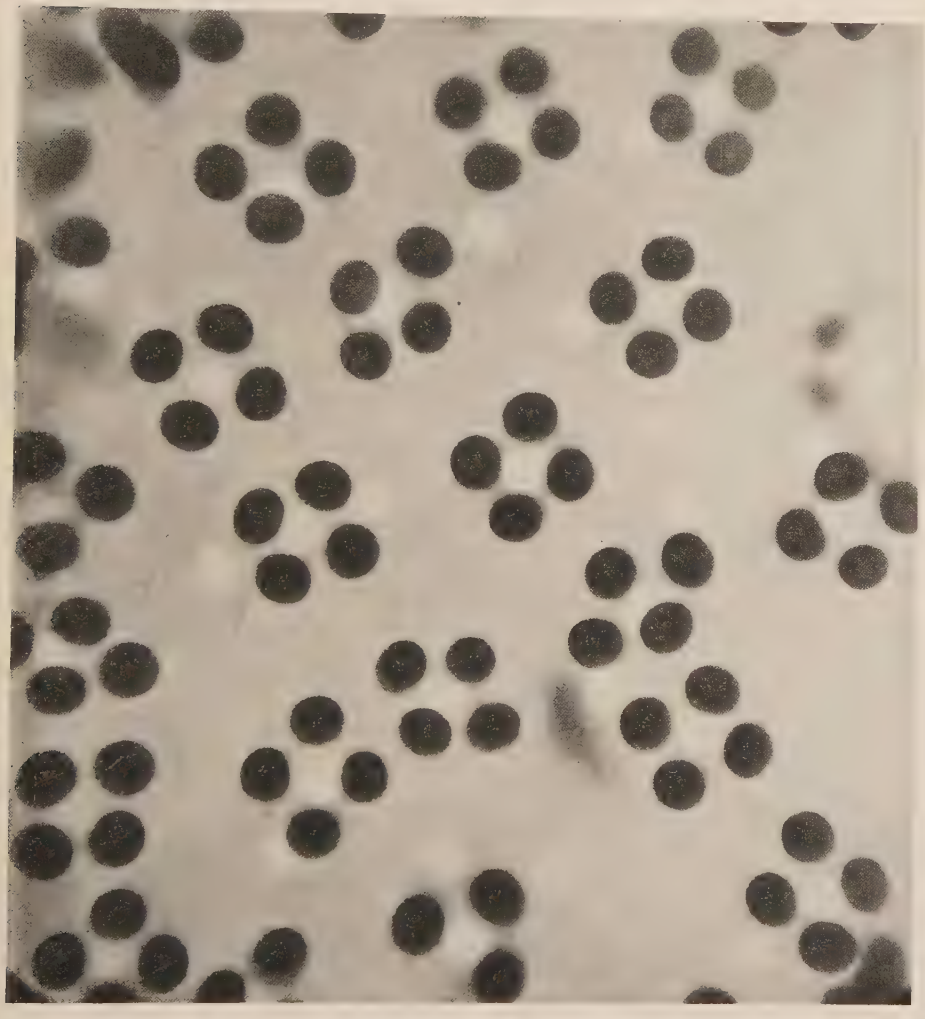


FIG. 128.—*Anellaria separata*. Photograph of part of a dark area of the hymenium of a living gill mounted in water. The plane of focus passes through the black spores of the present-generation basidia. Magnification, 640.

not hesitate, therefore, to give the details of the method by which it was made. A fruit-body was grown in the laboratory and from it, on the first day of spore-discharge, a gill was dissected carefully

[1] Except Fig. 107, p. 316, and Fig. 109, p. 319.

away. A drop of water was placed on a glass slide and on this the gill was floated. Another drop of water was then added at the side of the gill, whereupon the preparation was covered with a cover-glass. Under these conditions there was a layer of water between the under side of the gill and the cover-glass. On the upper side of the gill, as soon as the cover-glass had been applied, water began to make its way by capillary attraction over the hymenium, resistance to its passage being offered by the sterigmata and spores. When the water passed rapidly over the upper hymenial surface, as sometimes happened, the black spores were nearly all pulled off their sterigmata, whereby the whole preparation was spoiled: but, with a very gradual passage of the water, the black spores often remained on. Thus, by gradually passing water between the upper hymenial surface and the cover-glass, the former became covered with water without being ruined. The photograph reproduced in Fig. 128 was made from such a water-immersed preparation. In actually taking the photograph, a Leitz microphotographic apparatus was employed. A microscope was fitted with a Leitz ocular, No. 4, and an objective, No. 7; and above the tube the camera was placed so that it had a vertical arrangement. The light was given by a Leitz "Lilliput" arc-lamp which was set 3 feet from the microscope mirror. The part of the hymenium to be photographed was first focussed in the usual way. The light employed for this purpose came from the arc-lamp; but, in order to dim its rays, two sheets of glass, one blue and the other yellow, were set in front of it. After the focussing had been accomplished, the camera was swung into position at the top of the tube of the microscope. The piece of hymenium was then focussed on the ground-glass plate at the top of the camera. This plate was then removed and a photographic plate substituted for it. A black sheet of cardboard was next placed vertically against the base of the microscope so as to come between the mirror and the arc-lamp. Then the two sheets of coloured glass, already referred to, were removed from just in front of the arc-lamp. The carbons of the arc were then screwed close together so that the light coming from them was steadied. The cover of the photographic plate was then drawn out. Then the black sheet of cardboard was lifted away so

that the arc-light could shine on the mirror. The exposure was for about four seconds. At its end, the black cardboard sheet was replaced in its old position. Then the photographic plate was covered and taken to the dark-room for development. The magnification of the hymenium was 640 diameters.

Before the spores develop pigment, or even after they have become slightly brown, they have almost the same tint as the background made up of the gill substance. It is therefore difficult to get good photographs of the white areas of the mottled gill-surface. The clearest results of my efforts in this direction do not seem to me worthy of publication. The best idea of a white area may be obtained from such a *camera-lucida* drawing as is shown in Fig. 89 for *Panaeolus campanulatus* (p. 257).

We shall again return to the subject of photography of the hymenium in connection with the Coprini. With those fungi the gills were photographed without any immersion in water. The same method can be applied to *Anellaria separata*, but the results which I thus obtained were not so good as those obtained by the method just described.

CHAPTER XIII

PSALLIOTA CAMPESTRIS

Introductory Remarks—Occurrence of the Fruit-bodies—Fairy Rings—External Appearance of a Fruit-body—Evolution of Ammonia from Dead Fruit-bodies—General Organisation of the Fruit-body for the Production and Liberation of Spores—The Radial Arrangement of the Gills—The Number of the Gills—The Depth of the Gills—The Thickness of the Gills—The Ends of the Gills—The Gill-chamber and the Annulus—Conditions for the Origin of Fruit-bodies—The Fate of Rudimentary Fruit-bodies—Effect of Dry Weather on Development—The Spore-discharge Period and the Number of Spores—The Mushroom and the Panaeolus Sub-type—Text-book Illustrations of the Hymenium—The Mottling of the Gill Surface—Methods for Examining the Hymenium in Surface View—The Number and Size of the Spores on Individual Basidia—Rate and Mode of Development of the Spores of an Individual Basidium—An Analysis of the Hymenium of the Cultivated Mushroom—The Hymenium of the Wild Mushroom—*Camera-lucida* Studies of the Young Hymenium—*Camera-lucida* Studies of a Nearly Exhausted Hymenium—*Camera-lucida* Studies of a Completely Exhausted Hymenium—*Secotium agaricoides*

Introductory Remarks.—The present Chapter will treat of the production and liberation of spores in *Psalliota campestris*, the Common Mushroom (Fig. 129). The fruit-body of this fungus belongs to the Panaeolus Sub-type, and its hymenium is organised in all essentials exactly like that of *Panaeolus campanulatus* and *Stropharia semiglobata*. Since the Panaeolus Sub-type was described in great detail in connection with the two last-named species, it may seem superfluous that it should be dealt with any further. However, the Common Mushroom is so widely known all over the world as a familiar plant, is so celebrated as an article of food, and is so much employed in laboratory instruction, that it occupies a unique place among the Hymenomycetes. Moreover its structure, particularly in regard to the hymenium, has been described hitherto but very imperfectly. For all these reasons I have thought it desirable that I should give as full an account of the organisation

of the Mushroom as possible, always bearing in mind that the one dominant function of the fruit-body is the production and liberation of spores. This account will necessarily involve a repetition of a number of statements which have been made in connection with other representatives of the Panaeolus Sub-type, as well as of observations scattered through the pages of Volume I. The reader who is chiefly interested in the systematic description of the Aequi-hymeniiferous and Inaequi-hymeniiferous Types and of their Sub-types is therefore advised to pass over this Chapter and leave it to those who wish to increase their knowledge of a particular species. Among the new details of hymenial organisation which will be dealt with in the following pages may be mentioned : (1) the relation between the hymenium and the subhymenium, (2) the structure of monosporous and of bisporous basidia, (3) the arrangement of the spores on two adjacent bisporous basidia, and (4) the disappearance of exhausted basidia in late stages of hymenial activity. Also included in this Chapter will be found a new discussion of the form of the pileus, the stipe, and the gill-system, which is of general application to the Agaricineae.

In endeavouring to elucidate the organisation of the Aequi-hymeniiferous Type, my first attempts, made in 1911, were directed to the cultivated Mushroom. These partially failed owing to difficulties connected with the small size of the hymenial elements. I therefore turned my attention to *Panaeolus campanulatus* and *Stropharia semiglobata*, in which the basidia and paraphyses are relatively large ; and with these species my efforts, as we have seen in Chapters X and XI, were rewarded with a full measure of success. In 1916, I renewed my studies of the Mushroom ; and, in the light of a wide experience of hymenial organisation gained in the previous five years, I at once perceived that the fruit-bodies of this fungus have an organisation similar to that of the Panaeolus Sub-type. The magnification of the microscope used in working out the finer details of structure in the gills of *Panaeolus campanulatus* and *Stropharia semiglobata* had been 440. Now the diameter of the basidia of *Psalliota campestris* is only about one-half that of the basidia of those two species. In investigating the hymenium of the Mushroom, therefore, it became necessary at least to double

the magnification. The actual magnification employed was 1,040 diameters.

For all my investigations upon the Mushroom, I have used living material. Gills which have been fixed, stained, and cut with

Fig. 129.—*Psalliota campestris*, the Common Mushroom. From an English meadow. Photographed by Somerville Hastings. ⅓ natural size.

the microtome, hinder rather than help one in perceiving the finer relations of the hymenial elements to one another. In such sections, the ripe and nearly ripe spores are always torn from their sterigmata, thus leaving a number of basidia in a mutilated condition, and the basidia which still bear spores are relatively immature. Moreover, in a microtome section, it is often difficult or impossible to differentiate the hymenial elements from one another, owing to the fact that they were killed when being fixed and have therefore

lost their turgidity. The microtome method of making preparations is, as everybody knows, of the highest value for certain kinds of research, especially for cytology ; but, for my purposes, it proved quite unsuitable. I am inclined to believe that, if the microtome had never been invented, the progress in our knowledge of the general organisation of the hymenium of the Hymenomycetes would have been much greater by now than it actually is. The first successful investigators of the hymenium, such as Léveillé, Berkeley, and Schmitz, who flourished a century ago, studied their material in the living condition. My own work is in continuity with theirs.

Occurrence of the Fruit-bodies. Fairy Rings.—The fruit-bodies of *Psalliota campestris*, the Common Mushroom, occur more especially in pastures and other grassy places, where the mycelium apparently feeds upon organic débris consisting of the subterranean organs of grasses and perhaps other herbs, which are present in the turf. They also sometimes come up on lawns, in well-manured gardens, and in beds rich in turf and rotted horse manure, such as are used for growing tomatoes and cucumbers. In addition, Mushrooms are grown on a very large scale on artificial beds made of stable manure. In pastures, they usually occur singly and without any regular order in respect to one another, but sometimes they occur in so-called *fairy rings* (Fig. 130). Such rings I saw near Banbury, England, about the middle of August, in a hay-field which had been mown only a few weeks before. One of the rings was 1 yard in diameter, two others 2 yards, and one 3 yards. There were also a number of incomplete rings. Each ring consisted of a circular dark-green zone of grass from 8 inches to 1 foot across. From this zone both centrifugally and centripetally the grass was of a normal lighter green colour. There were several fruit-bodies coming up in each ring (*cf.* Fig. 131). On making excavations, I found that the soil consisted of a stiff red loam and that, just beneath the dark-green zone but nowhere else, the mycelium, interlaced with roots and rhizomes, could be traced downwards for a distance of 3 inches (*cf.* Figs. 132 and 133). From our general knowledge of fairy rings, we may conclude that the mycelium had started its existence in the centre of the ring, that it had grown centrifugally outwards each year,

and that, in all probability, it had produced a series of successive annual crops of fruit-bodies above the dark-green zone. Bayliss observed that in one of the rings of *Marasmius oreades*, the well-known Fairy Ring Fungus, where the radius of the ring was already nearly four and a half feet, the radial increase of size of the ring through the growth of the mycelium was in four successive years

Fig. 130.—Two fairy rings of *Psalliota* (= *Agaricus*) *tabularis*, containing large fruit-bodies about 15 cm. in diameter and of relatively uniform size. Photographed at Akron, California, U.S.A., June 7, 1909, by H. L. Shantz and R. L. Piemeisel. Courtesy of the United States Department of Agriculture.

6, 9·5, 10·5, and 13·5 inches respectively.[1] In other instances she found very similar results which showed that the tendency of each ring was to extend more and more rapidly as it gets older and as its radius increases. Probably the rings of *Psalliota campestris* behave very similarly. The ring which I found to have a diameter of 3 yards may well have been enlarging for six or seven years with accelerated speed. Owing to the rarity of fairy

[1] Jessie S. Bayliss, "Observations on *Marasmius oreades* and *Clitocybe gigantea* as Parasitic Fungi," *Journal of Economic Biology*, 1911, vol. vi, p. 118.

rings in connection with *Psalliota campestris*, at least so far as my own experience is concerned, it may be well perhaps to insist that the rings which I observed did as a matter of fact belong to this species and not to *Psalliota arvensis*. The fruit-bodies were quite typically those of the Common Mushroom, and not those of the Horse Mushroom. Shantz and Piemeisel [1] found numerous fairy rings formed by *Psalliota campestris* in grass-land near Yuma, California ; and, in one instance, as is shown in Fig. 131, they observed several Mushroom rings enclosed by a much larger ring formed by the mycelium of *Calvatia cyathiformis*. *Psalliota arvensis* sometimes also produces rings, and a good illustration of such a ring occurring in the United States is given by Atkinson.[2] I have seen similar rings at Malvern, England, many yards in diameter and dotted with the unmistakable, huge, white-topped fruit-bodies of the species in question. I have also observed some beautiful fairy rings of *Psalliota sylvicola*, indicated by numerous fruit-bodies, in a wood near Haslemere in England ; and Shantz and Piemeisel [3] found huge rings in eastern California formed by the mycelium of *Psalliota tabularis* (Fig. 130). It therefore appears that, under suitable conditions, there is a tendency for the formation of fairy rings in several species of the genus Psalliota. There can be no doubt that the mycelium of the fairy rings of *Psalliota campestris* is perennial and that it may live on for a number of years producing fruit-bodies annually. In this respect the vegetative part of the fungus is analogous to the creeping rhizomes of many Gramineae, Liliaceae, etc., which also have a perennial existence and serve as a basis for the annual production of a new crop of aerial shoots, flowers, and seeds.

In general, in a fairy ring occurring in a field there is usually an outer stimulated zone of green plants, a central more or less bare zone, and an inner somewhat wider stimulated zone, the stimulation making itself apparent in the increased height and greater greenness of the vegetation. According to Shantz and Piemeisel,

[1] H. L. Shantz and R. L. Piemeisel, " Fungus Fairy Rings in Eastern Colorado and their Effect on Vegetation," *Journ. of Agri. Research*, vol. xi, 1917.

[2] G. F. Atkinson, *Studies of American Fungi, Mushrooms, edible, poisonous*, etc., Ithaca, edition 2, 1901, Fig. 18, p. 20.

[3] Shantz and Piemeisel, *loc. cit.*

the bare zone is simply due to the fact that in dry weather the green plants in the zone are killed owing to the mycelium in the ground

Fig. 131.—Fairy rings formed by two Basidiomycetes in the short grass north-east of Yuma, California, U.S.A. The signs represent the positions of fruit-bodies. The large outer almost complete ring, which has a diameter of 65 metres, was formed by the mycelium of a Puff-ball, *Calvatia cyathiformis*. The clear discs on the outside of the ring represent the positions of fresh fruit-bodies and the black discs on the inside of the ring dry fruit-bodies of the previous year. Interrupting the continuity of the Puff-ball ring, and also within the area bounded by the Puff-ball ring, are numerous rings formed by the mycelium of *Psalliota campestris*—the Common Mushroom. Mapped by H. L. Shantz and R. L. Piemeisel. Courtesy of the United States Department of Agriculture.

beneath cutting off the supply of water from their roots, and the stimulated zones are due to the mycelium increasing the availability of the soil's nitrogenous contents. These observers have also shown that the subterranean mycelium has essentially the same

effect upon wheat plants in an arable field as upon wild grass plants in a natural sod (*cf.* Figs. 132 and 133).

In many well-grazed pastures in England, *Psalliota campestris* does not form fairy rings which can be clearly discerned, and the mushrooms occur either singly or in ill-defined associations. Such pastures, however, often produce mushrooms year after year. Under these conditions is the mycelium perennial, living on from year to year in the turf ? Or must we suppose that the pastures are annually re-infected from spores in such a way that each mycelium, in a single season, develops to maturity, produces a single

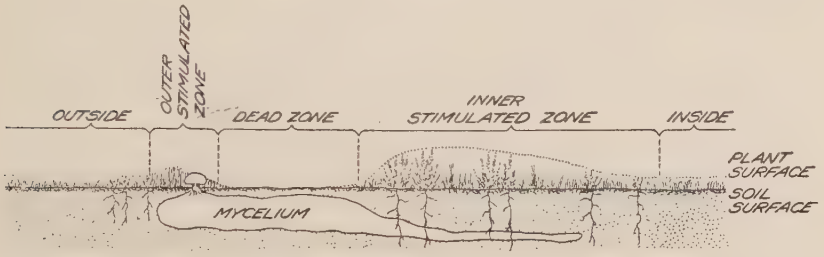


FIG. 132.—A vertical section through a fairy ring caused by the mycelium of *Psalliota* (= *Agaricus*) *tabularis*, in grass in eastern Colorado, U.S.A. The mycelium, which has produced a fruit-body in the outer stimulated zone, is progressing from right to left. Drawn by H. L. Shantz and R. L. Piemeisel. Courtesy of the United States Department of Agriculture.

crop of fruit-bodies, and then dies from exhaustion ? Doubtless, new infections of the turf take place occasionally. However, there is reason to suppose that a mycelium, when once it has been produced, often lives on from year to year just as it does in fairy rings but without giving rise to a ring. Ring-formation is only made possible by the turf being so even in its quality that the mycelium can develop centrifugally in an equal manner along all radii. In many fields the turf is organically uneven, owing to the occurrence of weeds, irregular grazing by animals, uneven drainage, uneven deposits of excrement or manure, heterogeneous character of the soil, or to the presence in it of various organisms other than herbage plants. In such fields the mycelium of *Psalliota campestris* must penetrate through the turf in an irregular manner ; but there is no reason why this irregular penetration should not often be continued perennially just as it is in fairy rings. I am therefore

inclined to believe that in fairy-ring-less pastures, where Mushrooms make their appearance year after year, much of the mycelium is perennial and capable of producing fruit-bodies annually.

It seems to me that, although much of the turf in certain fields may be capable of supporting the mycelium of *Psalliota campestris*, and although spores may be deposited upon it in great numbers, yet new infections from such spores only take place very rarely; and the same statement holds for *Marasmius oreades* and for other

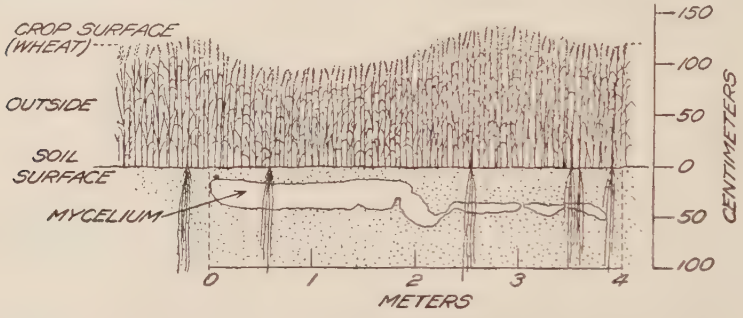


FIG. 133.—A vertical section through a fairy ring caused by the mycelium of *Psalliota* (= *Agaricus*) *tabularis* in a wheat field in 1915, a year of ample moisture supply. Colorado, U.S.A. Sketched by H. L. Shantz and R. L. Piemeisel. Courtesy of the United States Department of Agriculture.

ring-forming fungi. This view is based on the following reasoning. A fairy ring is produced from a mycelium which grows radially outwards from a single point and progressively exhausts its substratum. The older parts of the mycelium die progressively, death taking place in a radial direction. Thus a fairy ring, so far as the fungus is concerned, is a living zone of mycelium which develops centrifugally. This centrifugal growth continues often for a considerable number of years. Now the turf outside the ring is evidently extremely well suited to support the mycelium of the fungus, for otherwise it would not be progressively invaded. Yet each year the surface of this turf must receive a vast deposit of spores from the fruit-bodies occurring in the same pasture. The spores, although thus showered by the million on the top of ground perfectly suited for infection, rarely cause infection; for, if infection frequently took place, the turf outside the ring would quickly

become evenly occupied by the mycelium and all further ring-formation would be rendered impossible. The inevitable conclusion from this argument seems to be, therefore, that the spores of *Psalliota campestris*, *Marasmius oreades*, *Clitocybe gigantea*, and of other ring-forming fungi occurring in pastures, even when scattered in prodigious numbers over fields where the turf is capable of supporting the mycelium, rarely succeed in causing infection. The reasons for the enormous waste of spores under these conditions require further elucidation.

External Appearance of a Fruit-body.—The following description of the fruit-body of *Psalliota campestris* includes the field characters only. It has been compiled, in the light of my own observations, from the descriptions given by Fries, Berkeley, Greville, Stevenson, Massee, and Atkinson, with the object of combining fulness with accuracy. For illustrations of the fruit-bodies of the wild Mushroom, as found in pastures, the reader is referred to Figs. 129 and 134 (pp. 362, 377) in this Chapter and to Figs. 9 and 17 in Volume I (pp. 36 and 51).

The pileus is 5–13 cm. broad, at first rounded but, as expansion takes place, its top becomes first convex and then flat. The surface is at first smooth, presenting a soft, silky appearance from numerous loose fibrils, but later it is sometimes torn into triangular scales, especially as the fruit-body becomes old. The colour is usually white, but varies more or less to light brown, especially in the scaly forms where the scales may be quite prominent and dark brown. Sometimes the colour is brownish before the scales appear. The flesh is firm, thick, white, often more or less stained with reddish-brown, especially when bruised. The pellicle is extended slightly beyond the margin of the pileus and can be easily separated from the subjacent flesh.

The gills are free but rather close to the stipe, 0·6–1·6 cm. broad in the middle, of various lengths, closely set together so that the interlamellar spaces are narrow ; the longest gills are equally attenuated at both ends and ventricose. The colour of the gills in the button stage of the pileus is white, but at the time of expansion it is a beautiful pink. As the pileus becomes older and more and more expanded, the pink changes successively

to purple-brown, chocolate-brown, and finally to almost black. As soon as the pileus has expanded, the surface of each gill is seen to be mottled, owing to the fact that pigmented spores are present on the darker areas and unpigmented spores on the lighter areas. The mottling is somewhat fine in texture, but can easily be detected with the naked eye, and it persists for several days until the pileus is nearly exhausted. The edge of the gill is whitish and minutely denticulate.

The stipe is 5–10 cm. long, 1·2–2 cm. thick, bulbous when young, at maturity cylindrical but often tapering somewhat to the lower end ; sometimes it is thicker below than above or even sub-bulbous at the base. It is white. The flesh is solid except for the central core which is more or less stuffed with looser fibrils. The stipe is easily separated from the substance of the pileus.

The velum is thin, white, silky, and very fragile. It is stretched horizontally as the pileus expands and finally torn, so that an annulus is formed about the middle of the stipe while fragments cling to the pileus margin. The annulus is more or less sheathed to the stipe, margin spreading or reflexed, torn, often deciduous, shrivelling as the fruit-body ages and thus becoming more and more inconspicuous. Sometimes it is in the form of a cortina.

The spores are purple-brown, elliptical, 7–9 μ long, breadth and depth equal, each about 5–6 μ.

A fruit-body, when fresh, has a weak but pleasant odour and an excellent flavour when cooked for food. As soon as the pileus has ceased to shed spores, *i.e.* about the sixth day after expansion, the stipe and pileus both collapse and become converted rapidly into a very dark putrescent mass.

A few comments on the descriptions given by other authors will now be made. The colour of the gills is chiefly due to the cell-sap in all the cells. This sap is at first colourless but, as the pileus expands, it becomes pink. As the pileus flattens, the pink colour of the cell-sap changes to brown ; and, as the pileus ages, the brown colour of the cell-sap becomes progressively darker until it is almost black. Atkinson[1] states that the gills "soon become pink in colour and after the cap is expanded they quickly

[1] G. F. Atkinson, *loc. cit.*, p. 19.

become purple-brown, dark brown, and nearly black from the large number of spores on their surface." Although it is true that a certain number of waste spores do accumulate on the gills during the period of spore-discharge, yet it is incorrect to attribute the deepening of the colour of the gills chiefly to their presence. The change in colour of the gills is due in the main to the gradual darkening of the cell-sap of all the gill-elements. We have the same phenomenon in such Coprini as *Coprinus comatus* and *C. sterquilinus*. In these species, a pink cell-sap comes into existence shortly before the spores become produced or become pigmented; and, as the pileus grows older, just prior to the beginning of spore-discharge, the pink sap changes to a very deep brown. In the case of *Coprinus sterquilinus*, I have been able to prove experimentally that the sap-pigment arises through the action of an oxidising enzyme; and, doubtless, a similar biochemical cause is responsible for the colour changes in the gills of *Psalliota campestris*.

The mottling of the gills, which can be readily made out by anyone who looks for it, was observed by Berkeley,[1] but is not mentioned by Fries, Greville, Stevenson, Massee, or Atkinson.

Fries [2] described the gills as "saepe liquescentes," Stevenson [3] as "often deliquescent," and Massee [4] as "subdeliquescent." The gills, it is true, are very soft; but, while the spores are being shed, they remain firm and do not undergo deliquescence (autodigestion). In this they differ very markedly from the gills of the Coprini. However, as soon as they have become exhausted by discharging all their spores or have been killed by bruising or other injury, they quickly collapse and become reduced to a pulp, partly perhaps through the action of their own enzymes but chiefly owing to the attack of putrefactive bacteria. On the surface of a dead gill these bacteria multiply with extraordinary rapidity. The only trace of autodigestion in the living gill of a Mushroom is to be found in the collapse of the individual basidia shortly after each has shed its spores, and in the entire disappearance of many of the

[1] M. J. Berkeley, *The English Flora*, vol. v, Part II, Fungi, 1836, p. 107; also cited in Massee's *British Fungus-Flora*, London, vol. i, 1892, p. 411.

[2] E. Fries, *Monographia Hymenomycetum Sueciae*, Upsaliae, vol. i, 1857, p. 406.

[3] J. Stevenson, *Hymenomycetes Britannici*, London, vol. i, 1886, p. 306.

[4] G. Massee, *British Fungus-Flora*, London, vol. i, 1892, p. 411.

collapsed bodies of such basidia before the death of the gill as a whole. Further particulars in regard to this matter, however, will be given later on.

Evolution of Ammonia from Dead Fruit-bodies.—I placed three pilei of the Common Mushroom on the bottom of a crystallising dish which was about 8 inches wide, covered the dish with a glass plate, and kept the whole on a laboratory table at ordinary room temperatures. The pilei in the course of a few days died, collapsed, and became subjected to the action of putrefactive bacteria, which reduced them to a pulp and caused an exudation from them of a dark brown fluid. As soon as putrefaction was in full operation, a large amount of free ammonia was emitted. This gas, which rapidly turned red litmus paper blue, could easily be detected by its odour which was very characteristic and pungent, and it gave the usual reactions in chemical tests for ammonia. This experiment has been repeated in successive years, and I now use it to demonstrate to students that free ammonia may be liberated into the atmosphere through the action of putrefactive bacteria.

General Organisation of the Fruit-body for the Production and Liberation of Spores.—The hymenium or spore-producing layer is situated upon the under side of the pileus. This position is fraught with various advantages. The dominating one is that it favours the escape of the spores, for, when these have been shot a little distance from the basidia which have produced them, they fall into a free space beneath the pileus whence they can be carried away by the wind without meeting with any obstacle. The subpilear position of the hymenium also secures the protection of the basidia from falling rain, from too rapid loss of water by transpiration during dry weather, and from the direct heating effect of the sun's rays.[1]

The hymenium is situated on the surface of several hundreds of lamellae which are packed closely together. Each of these structures is shaped much like the blade of a pen-knife with the cutting edge directed downwards. The production of the lamellae throws the hymenium into a series of folds and therefore serves

[1] *Cf.* vol. i, 1909, pp. 21–24.

to increase very greatly, and yet very compactly and very economically, the area on the under side of the pileus available for the development of spores. In one fruit-body, which was 9·8 cm. in diameter, the gills were found to have an area of a little more than 20·04 times the area of the under surface of the pileus-flesh to which they were attached. The specific increase of hymenial surface due to the production of gills in this particular fruit-body was therefore 20·04.[1]

The stipe is an organ which serves to raise the pileus, and therefore also the hymenial layer upon the gills, to such a height that a considerable space comes into existence between the under side of the pileus and the surface of the ground. The presence of this space enables the wind or air currents to pass freely below the pileus and thus to carry away the falling spores. Since the spores, after emerging from the interlamellar spaces, fall in still air at the rate of about 1 mm. per second,[2] and since the free space beneath the pileus is often 50 to 70 mm. in depth, it is clear that even a very feeble lateral current of air is sufficient not only to prevent the spores from settling directly beneath the pileus but also to carry them for long distances before they come to earth. Everyone knows from observation what long distances thistledown or the hairy seeds of the Willow may travel on a windy day. Yet, in still air, the rate of fall of the spores of the Mushroom is much slower than that of any hairy fruits or seeds.[3] It is clear, therefore, that when the wind is at all strong the spores of the Mushroom must often be carried many miles before they settle. If in a particular fruit-body we suppose the free space between the base of the gills and the ground to be 6 cm., and if we take the approximate average velocity of fall of the spores to be 1·2 mm. per second, then a simple calculation shows that the approximate length of time required for the spores to fall from the base of the gills to the ground in still air would be 50 seconds, *i.e.* nearly a minute.[4] Now,

[1] *Cf.* vol. i, pp. 27–31. The total area of all the gills in this fruit-body was 195·2 square inches, *i.e.* upwards of a square foot.

[2] Vol. i, p. 180.

[3] In still air, it was found that the fruits of the Thistle, *Cnicus arvensis*, fall 104 times as fast as the spores of a wild Mushroom. *Vide* Chap. I, p. 39.

[4] Vol. i, p. 216.

if we suppose, as a matter of theory, that the surface of the ground is perfectly flat and that the wind is moving over its surface quite uniformly at a rate of only 5 miles per hour, then the spores, before coming to earth after leaving the base of the gills, would be carried a distance of not less than 365 feet. But, in nature, on windy days, it must often happen that a gust of wind, after sweeping beneath a pileus, becomes deflected upwards and bears innumerable spores to a great height into the atmosphere, in which case it may be some hours before many of them settle, during which time they would probably be carried for some scores of miles.

The adjustments by which the hymenial surfaces on the gills are placed in the optimum position for spore-liberation in the Mushroom are no less than four in number, and may be summarised as follows : (1) turning the pileus into an erect position by an upward curvature of the stipe ; (2) raising the pileus several centimetres above the ground by growth in length of the stipe ; (3) placing the gills with their long axes horizontal by an expansion of the pileus ; and (4) setting the median planes of the gills in vertical positions by the turning of the gills themselves about their lines of attachment to the pileus-flesh. The expansion of the pileus is due to causes inherent in the fruit-body itself, but the other movements are controlled by the external stimulus of gravity : the upward curvature of the stipe and its continued growth in a direction away from the earth's centre are phenomena of negative geotropism, whilst the movement of the gills about their lines of attachment is a phenomenon of positive geotropism.[1]

The flesh of both stipe and pileus is firm and massive. The fruit-body is thus endowed with considerable rigidity, so that it remains immovable even when the wind is blowing. This rigidity is necessary in order to keep the lamellae fixed in their nicely adjusted positions. If the fruit-body were to sway about with every breeze like grass stems, a vast number of spores would be prevented from escaping from the sides of the gills. The spores are shot out into the interlamellar spaces a horizontal distance of not more than about 0·1 mm.[2] In still air, after arriving at this distance from the gill, the spores make a sharp turn and then fall vertically

[1] Vol. i, pp. 50–56. [2] Vol. i, p. 142.

downwards. If, owing to insufficient rigidity of the whole fruit-body, the lamellae were permitted to oscillate about their normal positions, or if the pileus were suddenly tilted, a very large number of spores after being shot away from their sterigmata would, on falling, touch the sides of the lamellae, adhere there, and never escape into the free air beneath the pileus. In an investigation upon some fruit-bodies with gills having a depth of 5 mm. the following facts were elucidated. When the median planes of the gills are tilted about their lines of attachment to the pileus to an angle of 1° 30′ from the vertical, the spores can all escape down the interlamellar spaces. If the tilt be increased to 2° 30′, the *critical angle* is reached : all the spores can still make their way out between the gills, but with any increase in the tilt some of them fall upon the hymenium and adhere there. With a tilt of 5° half the spores are lost, and with a tilt of 9° 30′ four-fifths of them.[1] These particulars serve to emphasise the necessity for considerable rigidity in the fruit-body as a whole.

The rigidity of the stipe is due in part to the turgidity, density of arrangement, and mode of adherence of the long strings of hyphae making up its substance, but in part also to the fact that the stipe as a whole tends to have the form of a hollow cylinder.[2] In one variety of Mushroom which I cultivated in England, the core of the stipe was always distinctly hollow.[3] In the wild Mushroom the core is either hollow or stuffed with loose fibrils.

The firm and massive pileus-flesh, constructed of evenly-woven plectenchyma, is important from the mechanical point of view in that it supports the gills and keeps them fixed in a constant position during the several days of the spore-discharge period ; but it also has other functions : it serves to conduct nutriment to the gills during their development and constitutes a reservoir of water upon which the gills may draw according to their needs when they have attained maturity.

The form of the fruit-body of the Mushroom, or indeed of that of any other typical terrestrial agaric such as *Lepiota procera*, from the mechanical point of view, appears to be, within limits, the most

[1] Vol. i, pp. 39–40.
[2] Vol. i, pp. 41–45.
[3] Vol. i, Fig. 17, A and B, p. 51.

efficient possible, if one considers the conditions necessitated by the one great function to be performed, namely, the production and discharge of millions of basidiospores. A structure which must spread widely in a horizontal direction, so as to provide as great an area as possible on its lower surface for the hymenium, must be held firmly at a distance of several inches above the surface of the ground, so as to bring into existence a free space below the hymenium through which the wind may sweep ; and the supporting structure must be slender so as to economise fungus-substance as much as possible, so as to offer the least possible obstacle to the stream of escaping spores, and so as not to occupy a greater area of the valuable under-surface of the structure to be supported than is absolutely necessary. The structure to be supported is, of course, the pileus, and the supporting structure the stipe. There are various forms which one can think of as possible for both stipe and pileus, and various ways in which these bodies might be attached to one another. By mathematical calculations, the nature of which is well known to mechanical engineers, it can be shown that the fruit-body as a whole is most efficiently constructed, *i.e.* brings into play the smallest stresses and strains in its various parts, when : (1) the stipe has the form of a hollow cylinder, (2) the pileus has the form of a cone, (3) the axes of the stipe and of the pileus are vertical, and (4) the stipe is attached immediately under the centre of the lower side of the pileus. Since these characteristics are all found more or less perfectly embodied in the Mushroom, we must conclude that the general shape of this fruit-body approximates to the ideal.

In *Lepiota procera*, as shown in Figs. 14 and 15 in Volume I (pp. 44 and 45), the very large pileus remains in the form of a low upright cone during the whole period of spore-discharge. In *Psalliota campestris* the pileus, during expansion, also assumes the form of a low upright cone or plano-convex structure (Fig. 134, A), but subsequently its edges turn up so that finally the top of the pileus becomes flattened ; and then the cone is, as it were, turned upside down (Fig. 134, B). The turning up of the edge of the pileus causes the gills to be raised in such a way that their long axes are inclined upwards through a considerable angle. The disadvantage accruing

from the gills being thus upwardly inclined instead of remaining with their long axes directed horizontally lies in the fact that the vertical distances between the gills through which the spores (especially those liberated near the tops of the gills) have to fall are thereby increased, and that with these increases there is

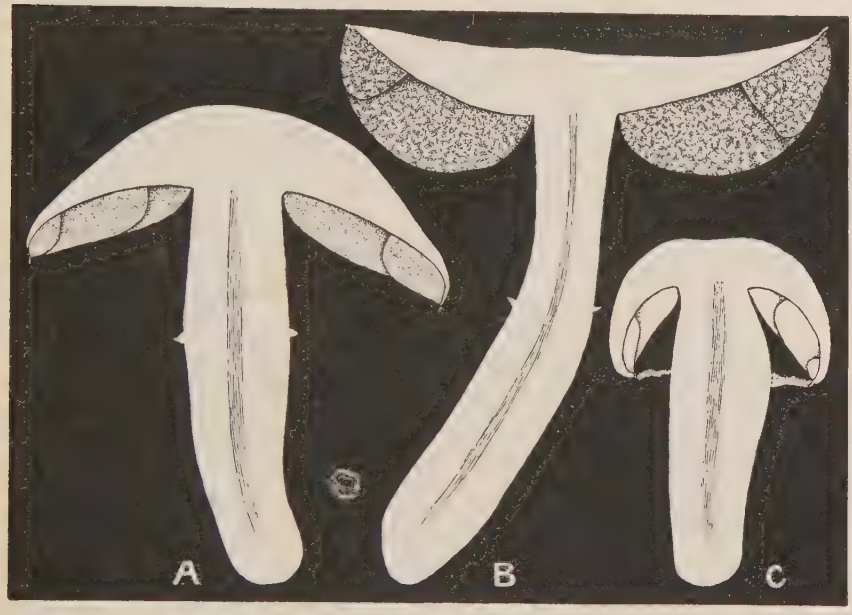


Fig. 134.—*Psalliota campestris*, wild form obtained in a pasture at Banbury, England. Sections through fruit-bodies to show the appearance of the gills at different ages. In C, where the gill-chamber is as yet unruptured, the surface of the gills has an even appearance. In A, where the pileus is expanding, the surface of the gills is faintly mottled. In B, where the pileus is fully expanded, the gills are very distinctly mottled. Natural size.

increased risk that the spores in passing down the very narrow interlamellar passages will touch the gill-sides and adhere to them ; but there is a distinct advantage gained, namely, that the gills as a whole, and therefore also the basidia, are raised an appreciable part of an inch. This extra elevation, obtained by sacrificing to a slight extent what we considered to be the ideal form of the pileus, permits of the free space beneath the gills being increased in depth, with the result that the wind has so much the better chance of carrying off the spores.

A flattening of the pileus, with a consequent raising of the gills, occurs toward the end of pileus expansion not only in the Common Mushroom, but in many other large Agaricineae. For *Amanita rubescens* it is shown photographically in Figs. 135 and 136.

The Radial Arrangement of the Gills. Granted that the

FIG. 135.—*Amanita rubescens*. A fruit-body with a convex, still expanding pileus. The annulus, which formed the base of the gill-chamber, is now hanging downwards and hence is not an obstacle to the falling spores. Photographed at Four Oaks, Warwickshire, by J. E. Titley. About $\frac{1}{3}$ natural size. The pileus was 4 inches in diameter.

lamellae are useful to the fruit-body in that they serve to increase the amount of surface available for the hymenium, yet we may still ask why they should be arranged in a radial manner. Why should the gills stretch along radii from the stipe to the periphery of the pileus and never form concentric bands ? I believe that the answer is as follows : (1) the radial arrangement involves a less complicated adjustment in securing that the lamellae shall look directly toward the earth than would the concentric one, and (2) the radial arrangement, with its radial interlamellar spaces,

subjects the gills to a lesser and more equal strain during the expansion of the pileus than the concentric one.

(1) As a pileus of a Mushroom opens out, its periphery moves away from the stipe and upwards about the stipe apex (Fig. 134). During this movement, the median planes of the lamellae remain

FIG. 136.—*Amanita rubescens.* The same fruit-body as that shown in Fig. 135, but one day older. The top of the pileus is now flat. The expansion of the pileus since the previous day has raised the gills and inclined them upwards, thus giving to the wind a better chance of carrying away the spores. Photographed at Four Oaks, Warwickshire, by J. E. Titley. About $\frac{1}{3}$ natural size. The pileus was 4 inches in diameter.

vertical, so that the hymenium on their sides continues to look slightly downwards. An upward movement of the whole pileus-periphery does not therefore seriously affect the escape of the spores which are being discharged from the basidia. But let us suppose that the lamellae in the closed pileus were to arise on the base of the pileus-flesh in the form of concentric bands. Then, as the pileus expanded, the median gill-planes would constantly alter their inclination to the vertical, and they could not take up their final vertical positions until the pileus-flesh had ceased to move.

The result would be that the beginning of spore-discharge would need to be considerably delayed or, if spore-discharge were to take place during the expansion of the pileus, there would be a great waste of spores, for a large proportion of the discharged spores would strike the gill-sides, adhere there, and never be carried off by the wind. One perceives that, with a concentric arrangement of the gills, the adjustments for securing that the hymenium shall look more or less downwards would be necessarily more complex, take longer to complete, and allow of less elasticity than with the radial arrangement.

(2) The peripheral boundary of the pileus of a Mushroom increases very greatly and rapidly as the pileus expands. If the gills, instead of having the radial arrangement, had the concentric one, the amount of stretching to which the gills would be subjected during the expansion of the pileus would be by no means equal, but would increase progressively and considerably from the innermost gill surrounding the stipe to the outermost gill at the periphery of the pileus. During the rapid expansion of the pileus, the outermost gills in particular would be subjected to great strain, and only by extraordinarily rapid growth could they respond to the demands made upon them by the rapid increase of the pileus-periphery. During the expansion of the pileus, the innermost concentric gills would require to lengthen their circumferences only very slightly, but the outermost ones would require to lengthen theirs relatively enormously. I cannot help thinking that the concentric arrangement of the gills, which would involve such an inequality in the development of the gills, would result in inefficiency in the production of spores, and that the radial arrangement, where all the gills are equally stretched in the radial direction, is on this account much to be preferred.

For the reasons given above we may conclude that the radial arrangement of the lamellae, as we actually have it in a Mushroom, is most beautifully adapted to secure the highest efficiency in the production and liberation of the spores.

The radial arrangement of the gills comes into existence during the development of the pileus in the following manner. The first gills to make their appearance in the very rudimentary pileus are

the long ones. As the pileus grows in size and the spaces at the pileus-periphery between the first-formed gills become wider, new and shorter gills are interpolated between the older ones ; and this process of gill-interpolation goes on continuously as spaces become provided until all the gills have been formed. The very shortest gills are always the last ones to appear. The determining factor in the origin of a new gill seems to be the divergence beyond a certain degree of two older gills. As soon as an interlamellar space has attained a certain width, a new gill-rudiment arises midway between them. It is owing to this mode of development of the gills in general that the wonderful system of lamellae on the under side of a mature Mushroom comes to be established ; and, by comprehending it, we can understand why it is that two gills never touch one another and why the interlamellar spaces are never reduced beyond a certain minimum and never exceed a certain maximum. The law of gill-development secures that the under side of the Mushroom shall be as crowded with lamellae as is consistent with the efficient discharge of the spores.

The Number of the Gills.—The number of gills in any gill-system varies from about 300 in small mushrooms to over 600 in large ones. It is dependent to a great extent upon the diameter of the pileus. This clearly follows from the consideration that as two long gills pass from the stipe to the periphery they diverge progressively more and more, and therefore leave room for the interpolation of more and more shorter gills.

A certain variety of the Common Mushroom was cultivated artificially on a bed of horse manure. A small mushroom which came up had a diameter in the fully expanded condition of 4·5 cm. It possessed in all about 320 gills : 120 long ones, 120 intermediate ones, and 80 very short ones. The spaces between the long and intermediate gills numbered 240, but they were so narrow that only one-third of them were divided by very short gills. The gill-system in this particular mushroom, therefore, consisted for the most part of gills of two lengths only. Four other larger mushrooms, each of which was approximately 8 cm. in diameter, possessed the following respective numbers of gills at the pileus-periphery : 509, 586, 616, and 628, *i.e.* the gills of these

larger mushrooms were twice, or somewhat more than twice, as numerous as those in the very small mushroom. The larger mushrooms had a gill-system which was everywhere made up of gills of at least three lengths : long, short, and shorter. while between the two last types of gills very short gills were frequently interpolated.

Other factors, besides the diameter of the pileus, which affect the number of the gills, are : the diameter of the stipe and the thickness of the gills where they adjoin the pileus-flesh. The thickness of the gills depends on their depth, for the deeper a gill is, since it is wedge-shaped in cross-section, the thicker it must be where it is attached to the pileus. With a given diameter for a pileus, therefore, the deeper the gills are, the greater space will each occupy below the pileus and the fewer there can be of them. I carefully compared two sets of fruit-bodies : (1) wild mushrooms gathered from a field near Birmingham, England, and (2) cultivated mushrooms of a particular variety grown artificially on a mushroom-bed. I found that, with fruit-bodies of the same diameter, the wild mushrooms had deeper and thicker but less numerous gills than the cultivated ones. The depth of the middle of the long gills in the wild mushrooms was 9 mm., whereas the corresponding depth in the cultivated mushrooms was only 6 mm. A wild mushroom with a diameter of about 8 cm. possessed about 413 gills and a cultivated one with an equal diameter about 600, the count in each case having included all the very smallest gills which could be clearly discerned at the pileus-periphery. It became obvious from this comparison and from others that, not merely theoretically but also actually, there is a relation between gill-depth and gill-number.

The close packing of the gills in one of the cultivated mushrooms is obvious from a glance at Fig. 137. This particular pileus was 6 cm. in diameter, but it was not yet quite fully expanded. It might perhaps have increased its diameter to 6·5 cm. if it had been left to continue its development upon the mushroom-bed. By throwing a photograph of this pileus on a screen from a lantern-slide, it became possible to count the gills at the stipe and at the pileus-periphery very exactly. The number of gills at the stipe was 132 and the number at the pileus-periphery

639. A wild mushroom which measured 9·2 cm. in diameter in the fully expanded condition and which was therefore considerably larger than the cultivated mushroom just considered, had almost exactly the same number of gills, namely, 134 at the stipe and 644 at the pileus-periphery. This comparison points to the conclusion that on equal spaces beneath the pileus the cultivated mushrooms tended to produce the larger number of gills.

Fig. 137.—*Psalliota campestris*, cultivated form. The pileus of a fruit-body photographed from below immediately after its removal from a mushroom bed. Notwithstanding the close packing of the gill-system, there are interlamellar spaces, into which the spores can be shot, between every pair of adjacent lamellae. Natural size.

Let us suppose that a pileus is endowed with perfect radial symmetry and on this supposition investigate the nature of its gill-system. Let the number of long gills, *i.e.* those which pass from the stipe to the pileus-periphery, be equal to x. Then, at a little distance from the stipe in the radial direction, owing to the gradual divergence of the long gills and the provision of the necessary interlamellar spaces, we should find a second set of gills, all of exactly the same length, regularly interpolated, one in each space or a total of x. The number of interlamellar spaces is now equal to $2x$. At a farther distance from the stipe, we should find a third set of gills interpolated, all of exactly equal length, one in each space or a total of $2x$. These by their presence would increase the number of spaces to $4x$. Still farther from the stipe we should find a fourth series of gills interpolated, all of exactly equal length, one in each space or a total of $4x$. If, still farther toward the pileus-periphery, a

fifth set of gills were present, they would number $8x$ and be interpolated in as many spaces. The total number of gills on the whole pileus would be the sum of

$$x + x + 2x + 4x + 8x$$

or, for n sets of gills,

$$x + x + 2x + 4x + 8x \ldots\ldots\ldots \text{to } n \text{ terms},$$

the sum of which is equal to

$$x \times 2^{n-1}.$$

If a perfectly symmetrical mushroom had 132 long gills and three distinct sets of gills, the total number of its gills would be

$$132 + 132 + 264 = 528$$

and, if it had four sets of gills, the total number of gills would be

$$132 + 132 + 264 + 528 = 1{,}056,$$

so that it is evident that every additional set of gills produced at the periphery of the pileus doubles the previous total. In nature, owing to the large number of factors which affect the growth of the cells making up the fruit-body, such perfect symmetry is never attained but only approximations thereto. The gills of each set vary considerably in length about a mean, and these variations become increasingly greater in each set as one proceeds from the stipe centrifugally.

If one examines the under side of a pileus, one finds that the gills are distinctly more crowded at the periphery than in the region of the stipe and a little way from it. It so happens in the pileus shown in Fig. 137 that the circumference of the pileus, where the gills end, is just four times the circumference of the stipe. There are 639 gills at the margin of the pileus. If the crowding of the gills were the same in the region of the stipe as at the pileus-periphery, then there ought to be 159 gills at the stipe; but, as a matter of fact, there are only 132. The extra crowding of the gills at the pileus-periphery is due to the fact that the gills in approaching their outer extremities become shallower and shallower (*cf.* Fig. 134, p. 377), and in accordance therewith thinner and thinner, so that each one occupies less and less space where it is attached to the pileus, much

less indeed than do the longer gills at their mid-lengths where they are deepest and thickest. The interlamellar spaces, as one can see from a glance at Fig. 137 (p. 383), are actually wider at the bottoms of the gills half-way between the stipe and pileus-periphery than at the periphery itself ; but at the tops of the gills where these adjoin the flesh they are all of approximately the same width.

The Depth of the Gills.—Let us now enquire why it is that the gills of a mushroom are so organised that they have a certain depth which varies but little about a mean. Why should not the gills be twice or three times as deep, or only one-half or one-third as deep ? What factors have led to the evolution of a depth such as we are now able to observe ? I am inclined to believe that the present gill-depth of *Psalliota campestris* has been gradually attained as a result of variations which have tended toward the production of the greatest amount of gill-surface with a given expenditure of mushroom substance. The considerations on which this view is based will now be elaborated.

Let us imagine a large wedge made of steel with the width and depth shown in the cross-section illustrated in Fig. 138 at ABC. Now let us suppose that we replace this wedge by two others which resemble the first in form but are only one-half as deep and wide (ADE + EFB). It is evident that the area of the lateral surface of the two new wedges taken together is the same as that of the first wedge but that their total volume is only one-half. Let us replace the two wedges by four others which resemble the two in form but are only one-half as deep and wide (AGH + HIE + EJK + KLB). The area of the lateral surface of the four wedges taken together is still equal to that of the original wedge, but the total volume has been reduced to a quarter. If we again replace the four wedges by eight, we shall find that, while once more there is no reduction of the original lateral surface, yet the volume is reduced to one-eighth. This process of substitution could be continued theoretically indefinitely, each substitution involving a reduction of the original volume to one-half but no alteration of the total lateral surface. Now let us suppose that it is desired to have the wedges of such a depth that with the least expenditure of material the surface of the lateral sides shall be collectively as

great as possible. Evidently, with the form of the wedge given, the area of the lateral sides cannot be increased, but the volume can be diminished by reducing the wedges in depth and increasing their

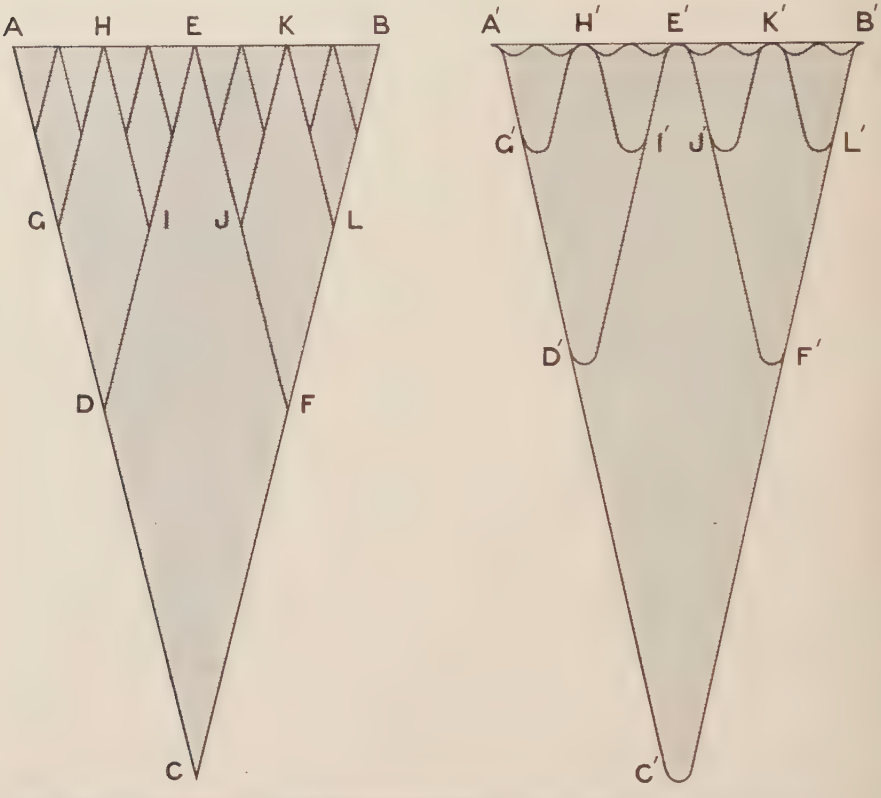


FIG. 138.—Diagrams to illustrate the relation of gill-depth to gill-surface and gill-volume. Left, a steel wedge in cross-section, with replacement by two, four, or eight wedges. Right, a gill in cross-section, with replacement by two, four, or eight gills. The eight small gills have much less surface than the eight small wedges.

number. One would therefore make the wedges as small as possible. The limit would be determined by human skill: it would be found that wedges could not be made less than a certain depth and yet retain their true symmetry.

Instead of a wedge of steel let us now consider a gill (Fig. 138, A′B′C′). A gill is wedge-shaped, but differs from the steel wedges already discussed in that its sides are slightly convex and in that it

is rounded both at the free edge and on each side where it adjoins its two neighbouring gills. Let A′B′C′ be the shape of a cross-section of a gill taken where the gill is deepest. Now let us replace this gill by two others which resemble the first in form and are of equal size (A′D′E′ + E′F′B′). The two gills will not meet at an acute angle, as did the two steel wedges, but the interlamellar space between them must be rounded as shown, so as to permit of the violent discharge of the spores for a distance of 0·1–0·2 mm. from the hymenium even at the narrowest part of the space, and so as to allow in addition for a margin of safety for the adjustment of the gill-planes in vertical directions even when the pileus happens to be slightly tilted (*cf.* Fig. 139, p. 390). Let us suppose that the radius of the rounded top of each interlamellar space, for the reasons given, is not to be reduced beyond 0·25 mm. Then we can speak of the narrowest portion of the interlamellar space as having a minimum width of 0·5 mm. Let us now replace the two gills by four. The new interlamellar spaces must be as wide as the old ones, *i.e.* 0·5 mm. wide at the top. Again, let us replace the four gills by eight. Here again, the seven interlamellar spaces all have a minimum width at the top of 0·5 mm. We thus see that, as the gills are progressively diminished in size, the minimum width of the interlamellar spaces remains constant. The gills, as they become more and more numerous and shallower, tend to be less and less like the original gill and more and more like rounded ridges, their exterior reminding one of the waves on the surface of water. If the process of substitution were to be continued, the gills would eventually disappear and the hymenium become perfectly flat. It is evident, therefore, that, unlike what was found to happen with the steel wedges, reduction of gill-depth with increase in gill-number leads to a very considerable reduction of the absolute amount of gill-surface. The greatest amount of gill-surface is possessed by the original gill A′B′C′, a slightly less amount by the two gills A′D′E′ + E′F′B′, and progressively less amounts with every increase of gill-number until the gill-substance has been reduced to zero. We may regard two tendencies as having had effect in leading to the establishment of the particular gill-depth which we find in *Psalliota campestris* at the present day : (1) a tendency to increase the absolute amount

of hymenial surface, and (2) a tendency to economise gill-substance. Now these tendencies are antagonistic, and the gills, as they exist to-day, embody within them a compromise between the two. If the gills were four times as deep as they actually are, more than four times as much substance would need to be put into each of these deeper gills than was present in the shallower gills which each deeper one would replace, while the actual increase of hymenial surface would be very slight. The absolute amount of increase of fruit-body substance with this increased depth of the gills would be relatively considerable, for the volume and weight of the whole gill-system would be increased by about four times. If the gills were only one-quarter as deep as they actually are, somewhat less than one-quarter of the substance present in one of the original gills would be put into the shallower gills which would replace it, but at the same time the decrease in the area of the hymenial surface would be considerable. The absolute diminution of fruit-body substance would be relatively inconsiderable and it would be purchased at the cost of a marked decrease in hymenial area. Owing to the fact that in the course of evolution a certain percentage of fruit-body substance in *Psalliota campestris* has been converted into deep and narrow gills, the hymenial surface has been increased about twenty times.[1] It seems to me, however, very probable that a further increase in the percentage of fruit-body substance put into gills would not be advantageous, owing to the fact, sufficiently indicated above, that the deeper the gills become the less the gain in surface relatively to the expenditure of gill substance.[2]

The Thickness of the Gills.—The amount of hymenial surface on the under side of a pileus is decided not merely by the depth of the gills but also by their thickness. With a constant depth, the thinner the gills, the more numerous can they be and the greater will be the hymenial area on their exterior collectively. As if with the object of producing as extended an hymenium as possible, the

[1] Vol. i, 1909, pp. 30–31.

[2] The geometrical principles relating to hymenial surface and gill-depth, which have been dealt with above, have been illustrated mathematically in an interesting manner by my colleague, Dr. C. D. Miller; but the mathematics involved would be considered by most mycologists as very abstruse. I believe that Dr. Miller intends to send his paper to one of the mathematical periodicals.

gills of *Psalliota campestris* are extremely thin, and it is doubtful if they could be appreciably thinner and yet continue to facilitate the free escape of the spores. A Mushroom was gathered from a field near Birmingham, England, and some tangential sections were cut through the pileus so as to pass vertically downwards through the region of the long gills at their deepest part, which happened to be 7 mm. deep. In cutting the sections it was impossible to avoid bending the gills somewhat, so that their median planes came to be no longer straight. Two of these sections, which were of course still living, were very carefully sketched with a magnification of sixty with the help of a *camera lucida*. Fig. 139 shows these *camera-lucida* drawings after they had been adjusted to the extent of straightening the gills so as to give these the alignment which they had in nature. With the aid of this Figure let us now consider the thickness of a typical long gill. The thinnest part of the gill is at its free edge. Just above this edge the actual thickness is reduced to 0·15 mm., and it could scarcely be thinner, owing to the fact that the gill-substance is bound to include two hymenial layers, two subhymenial layers, and at least some tramal hyphae. A quarter of the way up the gill, the thickness becomes increased to 0·25 mm., half way up to 0·3 mm., and just below the interlamellar sinuses at the top to 0·43 mm. The two sides of the gill converge from above downwards at a very acute angle which increases in size from above downwards. This angle in the upper part of the gill is only about 1°, but toward the middle of the gill it becomes increased to about 2°, whilst in the lower part of the gill it becomes 4°. The convergence of the two sides of every gill is of the greatest importance, for it is owing to its existence that every part of the hymenium on the under side of a normally adjusted pileus comes to look more or less downwards toward the earth, with the result that every small portion of the hymenium (every square mm.) can produce and liberate spores simultaneously during the whole period of spore-discharge.

In *Marasmius oreades*, many Hygrophori, Russulae, etc., the gills are much thicker relatively to their depth than in *Psalliota campestris*, or, to state the same thing in another way : the angle of convergence of the sides of the gills is considerably greater in

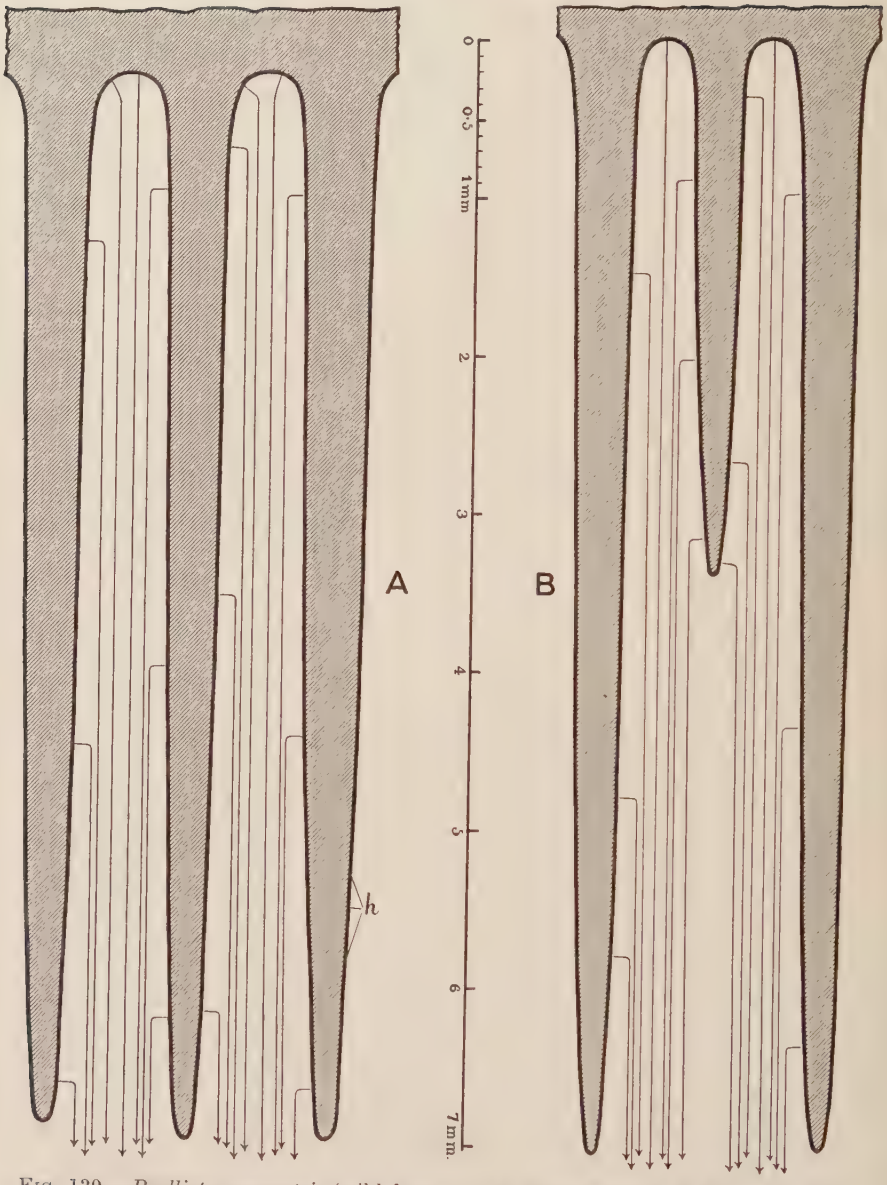


FIG. 139.—*Psalliota campestris* (wild form). Two cross-sections of gills. To show exactly the angle of convergence of the opposite sides of each gill and the shape of the interlamellar spaces as they are under field conditions. In cutting the sections of the freshly-gathered living mushroom with a hand-razor, each gill became unavoidably slightly curved to one side. The sections were mounted in water. *Camera-lucida* drawings were then made which were subsequently very carefully adjusted so as to make each gill look vertically downwards as shown above. *h*, the hymenium. The trajectories or sporabolas of a few spores, as they are in still air, are indicated by the arrows. The gills were originally 7 mm. deep. The scale enables one to measure their thickness at various depths.

these fungi than in the Common Mushroom. On the other hand, there are some Agaricineae which have thinner gills than *Psalliota campestris*, namely, the Coprini. In these, however, the gills are parallel-sided or subparallel-sided, and associated with this parallel-sidedness we find a special arrangement for the production and liberation of spores which is quite different from that in the Mushroom. If a Mushroom had parallel-sided gills with a thickness say of 0·2 mm., and its hymenium continued to be active everywhere at one and the same time, then, unless the gills could be kept practically quite vertical during the whole period of spore-discharge, a great many spores would be wasted. Suppose that a gill of a Mushroom were parallel-sided and 7 mm. deep and that the spores were shot out from the gill-sides to an average distance of 0·1 mm. Then, if the median planes of the gills were to diverge from the vertical by an angle of only 0·8°, which represents a slope just exceeding one in seventy, most of the spores on the upward-looking side of the gill would fail to escape from the pileus. It is evident that the margin of safety necessary for compensating for irregularities in development in such a case would be too small. In Mushrooms, as we actually find them in the field, the lower part of the gills can be bent from the vertical by an angle exceeding 2° and still all the spores can escape. In a former investigation, of which an account was given in Volume I, the critical angle of tilt for the gills of a particular Mushroom was found to be 2·5°.[1] The discussion just given may be taken as supporting the view that in *Psalliota campestris* the gills, provided they are to continue to liberate their spores successfully, have probably become reduced to their minimum thickness.

The Ends of the Gills.—We have now to account for the fact that the gills, when observed in lateral view (Fig. 134, p. 377), are deepest toward the middle and become narrowed down to a vanishing point at each end.

The narrowing of the gills toward the pileus-periphery, from the mechanical point of view, has the same significance as the corresponding thinning out of the pileus-flesh, *i.e.* it is in accordance with the mechanical requirements of the fruit-body as a whole. From

[1] Vol. i, p. 40.

the developmental and nutritional points of view, it also seems fitting that the gills should become shallower and shallower as the pileus-flesh immediately above them becomes progressively diminished in thickness beyond a certain point.

The narrowing of the gills in the neighbourhood of the stipe has an entirely different significance from the narrowing at the pileus-periphery. The gills are cut away from the stipe in such a way as to permit of their being raised through an angle of about 90° during the rapid expansion of the pileus, without their being subjected to strains which would tear them. The question of the relation of the gills to the stipe in Agaricineae in general, however, will be dealt with more fully in Volume IV.

The Gill-chamber and the Annulus.—The gills of a Mushroom are protected during their development and during the first stages of the expansion of the pileus by being enclosed in a gill-chamber. The wall of this chamber at the top and sides consists of the pileus-flesh and at the bottom of the *velum partiale* (Fig. 134, C, p. 377; also Fig. 140, D, F). As the pileus expands, the floor of the gill-chamber becomes drawn out horizontally into an extended but very thin and fragile membrane which, with further stretching, breaks, so that fragments of the velum are carried away upon the edge of the pileus (Fig. 137, p. 383) and an annulus is left surrounding the stipe (Fig. 134; also Fig. 140, A, B, H, I). The base of the thin membrane which closes the gill-chamber during the earlier stages of expansion, is, at its origin, a tubular structure ensheathing and apparently forming part of the outside of the stipe enclosed within the chamber. This sheath is pulled away from the stipe from below upwards during the expansion of the pileus (Fig. 140, B, C, E, F). The region of the stipe from which the sheath has been pulled can be distinguished in some field Mushrooms by its roughened surface, which indicates where cleavage took place: to its upper edge the annulus is attached, while at its lower edge there is not infrequently a trace of a second ring (Fig. 140, A). The origin of the roughened region and of the two annuli may best be realised by a reference to the semi-diagrammatic drawing given in Fig. 140, B, where the arrows indicate the movements which have taken place. Fig. 140, E, shows the exterior of a young Mushroom in which the

floor of the gill-chamber is actually in course of formation from the sheath, and in which an inferior annulus can be clearly discerned.

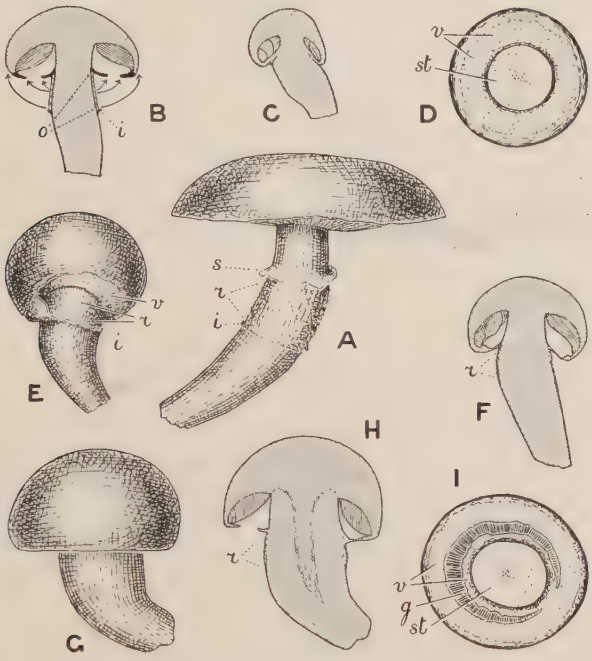


Fig. 140.—*Psalliota campestris.* From a field at Redditch, England. To show the occasional formation of an inferior annulus in addition to the superior annulus. A, a mature fruit-body, shedding spores, having a superior annulus *s*, a slight inferior annulus *i*, and a roughened area *r*. B, a diagrammatic vertical section to indicate the mode of origin of a double annulus: the velum has moved in the direction shown by the arrows from its position, *o*, and has left a slight inferior ring, *i*, behind. C, a very young fruit-body with the gills filling the gill-chamber; the velum is about to be pulled outwards away from the stipe. D, the under surface of a young fruit-body with the velum, *v*, closing the gill-chamber; *st*, the stipe. E, a young fruit-body which has just formed an inferior annulus, *i*, but in which the velum, *v*, still closes the gill-chamber; *r*, a roughened area formed by the pulling-away of the velum. F, a vertical section through a young fruit-body showing the gill-chamber closed by the velum which is being pulled away from the stipe leaving a roughened area, *r*. G, an external view of a young fruit-body. H, a vertical section of G, showing the velum forming the annulus; *r*, a roughened area like that of F. I, the under surface of the pileus of G and H, showing the gills, *g*, in the gill-chamber through a rent in the velum *v*; *st*, the stipe. ⅔ natural size.

The existence of a gill-chamber causes the gills, during their development, to be subjected to more even conditions of temperature and moisture than would be possible in its absence. The chamber floor also bars out from access to the gills—the most nutritious and vulnerable parts of the whole fruit-body—such small marauding animals as Fungus Gnats (Mycetophilidae), Springtails (Collembola), and Mites (Arachnida); and it also keeps away Bacteria and the spores of parasitic Fungi. The development of a gill-chamber which persists until spore-discharge is about to begin, *i.e.* until the last possible moment when it can be of service, is a beautiful contrivance which was probably added in a late stage of the evolution of the Mushroom. The annulus, owing to its delicacy, shrivels up soon after its definite formation and so comes to offer but a very slight obstacle to the removal of the falling spores by the wind.

Conditions for the Origin of Fruit-bodies.—The conditions under which the fruit-bodies of *Psalliota campestris* come into existence in the first place are not as yet by any means fully understood. We know that the mycelium vegetates in the substratum of turf or rotted horse manure for some weeks or months and that it then rapidly produces mushrooms. The mushrooms never arise at any depth in the substratum, but always at its surface. Two questions in this connection await an answer: (1) what internal changes cause the mycelium to proceed from the vegetative to the reproductive stage, and (2) what external stimulus decides that the fruit-bodies, when formed, shall arise at the surface of the substratum and nowhere else? In the absence of exact knowledge our answers to these questions can only be speculative.

The recent investigations of Mlle Bensaude, Hans Kniep, and Miss Mounce have proved conclusively that in the Hymenomycetes, as in the Phycomycetes, some species are homothallic and others heterothallic.[1] In a homothallic species, *e.g. Coprinus sterquilinus*, fruit-bodies are produced rapidly and perfectly upon a mycelium of monosporous origin. On the other hand, in a heterothallic species, *e.g. Coprinus fimetarius*, *Schizophyllum commune*, and *Coprinus lagopus*, this is usually not the case. Thus, according

[1] For a detailed treatment of the problem of sex in Hymenomycetes *vide infra*, vol. iv, Chapters on Sex.

to Mlle Bensaude,[1] monosporous cultures of *Coprinus fimetarius* are quite infertile ; according to Hans Kniep,[2] monosporous cultures of *Schizophyllum commune* are usually, although not always, infertile ; and according to Miss Mounce,[3] in *Coprinus lagopus*, while fruit-bodies arise on monosporous mycelia, such fruit-bodies often develop very few spores or even no spores at all. In all these heterothallic species, however, fruit-bodies are developed rapidly and perfectly upon secondary mycelia, *i.e.* mycelia derived from the union of two monosporous mycelia presumably of opposite sex. It thus appears that, in the heterothallic Hymenomycetes, the production of fruit-bodies is largely dependent upon the occurrence of a sexual act taking place between two mycelia presumably of opposite sex. We may therefore ask : Is *Psalliota campestris* homothallic or heterothallic ? If it is homothallic, then, doubtless, its fruit-bodies can be produced on mycelia of monosporous origin. If, however, it is heterothallic, then probably one of the conditions for the normal production of its fruit-bodies is the union of two mycelia of opposite sex. No one has attempted to obtain fruit-bodies from Mushroom spawn derived from a single Mushroom spore ; so that, for the present, in respect to *Psalliota campestris*, we lack knowledge which is vital for a full understanding of the conditions governing fruit-body formation.

I took some mycelium from a Mushroom bed and examined its hyphae with the microscope. I did not find any clamp-connections either in the independent hyphae or in those making up the mycelial cords. Mlle Bensaude [4] and Hans Kniep [5] have shown that the formation of clamp-connections in Coprinus, etc., stands in intimate relation with the conjugate division of a pair of nuclei, so that

[1] Mathilde Bensaude, *Recherches sur le cycle évolutif et la sexualité chez les Basidiomycètes*, Nemours, 1918, pp. 1–156.

[2] Hans Kniep, " Über morphologische und physiologische Geschlechtsdifferenzierung," *Verhandl. der Physikal.-med. Gesellschaft zu Würzburg*, 1919, pp. 8–16.

[3] Irene Mounce, (1) " Homothallism and the Production of Fruit-bodies by Monosporous Mycelia in the Genus Coprinus," *Trans. Brit. Myc. Soc.*, vol. vii, 1921, pp. 198–217 ; (2) " Homothallism and Heterothallism in the Genus Coprinus," *ibid.*, 1922, pp. 256–269.

[4] M. Bensaude, *loc. cit.*

[5] H. Kniep, " Beiträge zur Kenntnis der Hymenomyceten, III und IV," *Zeitschr. f. Botanik*, Bd. VII, 1915, and Bd. VIII, 1916.

clamp-connections are a sign that the nuclei in the hyphae are paired. Max Hirmer[1] has observed that the cells of the stipe and pileus-flesh of *Psalliota campestris* contain not pairs of nuclei, but groups of individual nuclei numbering up to eleven in each group. The absence of clamp-connections in the mycelium of a Mushroom bed is therefore probably due to the fact that the nuclei are not paired but exist in little groups. In many Hymenomycetes, the occurrence of the nuclei in pairs in the mycelium and the formation of clamp-connections appear to be prerequisites for fruit-body formation, but this is not so for *Psalliota campestris*. The reduction of the nuclear groups in the cells of a fruit-body of the Mushroom takes place, according to Hirmer, in the gills, and is accomplished by the time the subhymenium is formed.[2] This allows of a single pair of nuclei entering each basidium. Here nuclear fusion takes place in the usual manner.

There are doubtless other conditions than that of the correct arrangement of the nuclei, which are necessary for the production of fruit-bodies by a mycelium. It appears that a mycelium never begins to form fruit-bodies until its hyphae have accumulated protoplasm laden with food materials, sufficient in amount to ensure that any reproductive effort shall not utterly fail through lack of constructive materials. Perhaps, therefore, the mycelium is subjected to an internal stimulus of such a kind that each hypha has a certain effect on the whole mycelium in that it stimulates it to begin the process of fruit-body formation; and, perhaps, a reproductive effort on the part of the mycelium as a whole is only begun when the number of hyphae has become so large that the cumulative stimulus provided by all the hyphae exceeds a certain limit.

Let us suppose that the older part of a mycelium which has been vegetating for some weeks in the turf of a pasture has received a stimulus of such strength that the reaction must be a reproductive effort. We may take it that it is impossible for the mycelium to produce fruit-bodies at once owing to the fact that the external

[1] Max Hirmer, "Zur Kenntnis der Vielkernigkeit der Autobasidiomyzeten, I," *Zeitschrift für Botanik*, Jahrg. XII, 1920, pp. 668–669.

[2] *Ibid.*

conditions beneath the surface of the soil are not favourable thereto. The first reaction of the subterranean mycelium appears to be the formation of a network of cord-like strands. Probably these strands serve as a reservoir for the protoplasm and other materials which are to be put into the fruit-bodies ; and doubtless they are produced at the expense of substances supplied by the distant and actively-growing hyphae which are still attacking the substratum and extracting from it its nutriment. Certain of these strands, during their formation, grow upwards until they reach the surface of the soil and, as we know from observation upon artificial mushroom-beds made of soil-covered horse manure, can penetrate through an inch or more of non-nutritious compact soil or even through sand. This upward growth of mycelial strands absorbs both material and energy, but it is absolutely necessary in order that the reproductive bodies may be formed at the surface of the ground, where alone the spores may be liberated so as to secure their dispersal by the wind. One may ask whether or not the upward direction of growth of some of the strands is due to negative geotropism. Now, on artificial beds having various shapes with surfaces at the sides and bottom, mushrooms may arise anywhere on the surface (Vol. I, Fig. 17, p. 51). I am therefore inclined to believe that the strands grow upwards to the surface of the soil in fields not as a response to the stimulus of gravity but for some other reason. It is not improbable that the upward growth is purely a matter of chance. The mycelium, owing to its wonderful power of branching and to the apical growth of its hyphae, doubtless tends to penetrate through the interstices of the soil in all directions of space. This being so, some of the hyphae must make their way upwards. The strands are then formed about these hyphae. After being formed the strands immediately proceed to the formation of rudimentary fruit-bodies.

Why should the rudimentary fruit-bodies never be formed anywhere else than at the surface of the soil ? We can only suppose that this position is decided by the reaction of the mycelium to one or more external stimuli or by the absence of mechanical pressure. The stimuli most likely to be involved seem to be light, moisture, or atmospheric gases. Now light is unnecessary for the

formation of fruit-bodies ; for, as every mushroom-grower knows, mushrooms can be reared in perfectly dark cellars and caves where not a ray of light enters. When the mycelial strands approach the surface of the soil, they are liable to lose considerable quantities of water by transpiration, for the free air above the soil is usually much less moist than the air in the soil. This increased transpiration may well be one of the conditions favouring fruit-body formation. The production of fruit-bodies at the surface of the soil may be due in part to a stimulus provided by the gaseous environment. The soil must be considerably richer in carbon dioxide and other gases produced by the decomposition of organic matter, and at the same time poorer in oxygen, than the free air above it. Another point of difference between the gases in the soil and those of the free air is that the latter are in constant motion owing to air currents and the wind, while the former are relatively still. If the change of gaseous environment should be shown by future experiment to be the cause of the formation of fruit-bodies at the surface of the soil, its exact mode of operation will require detailed analysis. At or very near to the surface of the soil the mycelial strands are freer from mechanical pressure than well below it ; and it is therefore possible that mechanical freedom is also a factor in deciding the place of origin of the fruit-bodies. Here again there is room for an experimental enquiry.[1]

The Fate of Rudimentary Fruit-bodies.—On artificial mushroom-beds, a great many rudimentary fruit-bodies are produced for every one that comes to maturity : "many are called, but few are chosen." Perhaps there are at least fifty rudimentary fruit-bodies brought into existence for every one which ultimately liberates spores. No doubt the same thing happens in nature, although in pastures it is usually impossible to observe any fruit-bodies at all in their very earliest stages of development, owing to their being hidden by herbage. It seems to me that there is a considerable advantage in the formation of so many rudiments, notwithstanding that the vast majority of them are always destined to suffer abortion. The surface of the ground is an external condition

[1] For an experimental enquiry into the cause of the position of origin of the fruit-bodies of *Coprinus sterquilinus, vide* vol. iii, Chap. IV.

which the fungus plant is unable to alter. So far as the fungus is concerned, it may be beset with irregularly disposed mechanical obstacles, it may be divided into moister and drier spots, it may harbour lurking enemies, or be crushed down locally by the feet of herbivorous animals. The mycelium, on arriving at the surface of the substratum, gives rise to a considerable number of rudimentary fruit-bodies which at first are all alike ; but very soon a few, which occupy the most favourable situations for further growth, draw to themselves the nutriment available in the mycelial strands and thus rapidly increase in size. Most of the other rudiments not so favoured cease to draw nutriment to themselves and soon wither. It is not unlikely that some of the protoplasm of the rudiments which become aborted is passed back again into the mycelium, so that it may not be wasted, but ultimately finds its way into the favoured fruit-bodies which are destined to develop to maturity and thus propagate the species. By forming a large number of rudimentary fruit-bodies at relatively little expense in material and energy, the mycelium, as it were, carries out a reconnaissance of the nature of the substratum-surface and finally produces its effective reproductive organs only at the most favourable points.

Effect of Dry Weather on Development.—I think it probable that, in nature, the rudimentary fruit-bodies, like those of *Coprinus niveus* and certain other coprophilous fungi which I have actually observed, often have their development interrupted by lack of moisture. If during what may be called the mushroom season the weather continues dry, as everybody knows, no mushrooms appear. If, after such a dry spell, the weather breaks and heavy rain descends for a day or two so that the pastures are soaked, then large numbers of mushrooms make their appearance in the course of a very few days. I am inclined to believe that, when events happen in this way, the mushrooms are already present during the dry weather in the form of rudiments at the surface of the ground, but that their further development and final expansion have been delayed by drought which has temporarily checked the supply of constructive materials coming up from the mycelial strands. If the fruit-bodies which appear after a rainy day in

summer were to *begin* their development only after the soil had become watered, probably they would not appear in the pastures under the most favourable circumstances for at least ten days. The early stages of fruit-body development take place very slowly and cannot be hurried beyond a certain pace. The growth of a fruit-body in size undergoes acceleration from day to day, and the last stage, in which the stipe elongates and the pileus expands, is passed through so rapidly that many people are apt to think that a mushroom completes its full development in a single night. The rapidity of the expansion of a mushroom in its final phase of growth has been proverbial from the most ancient times and is, of course, based on the observations of the mushroom-gatherer bent on booty for the table ; but it must not be forgotten that this marvel of nature is only the climax of many days of slow and steady, although usually invisible, developmental progress.

The Spore-discharge Period and the Number of Spores.—The length of time occupied by any fruit-body in the discharge of spores may be conveniently called the spore-discharge period.[1] In order to determine this period for *Psalliota campestris* recourse was had to the following procedure. Two clods of turf each bearing a single mushroom, which was just bursting its gill-chamber and undergoing rapid expansion, were dug up in a field with great care so as not to injure the fungi in any way, and were removed to a potting-shed. Here each clod, which was about 5 inches in diameter and 5 inches deep, was inserted in an 8-inch pot and packed below and at the sides with wet soil, so that each mushroom took up a vertical position similar to that which it had had in nature. Each pot was then covered by a similar but inverted pot, and the hole at the top was partially closed with a plug of cotton-wool. The two preparations were then removed to a somewhat cool room in a house which was temporarily used as a laboratory. Thereupon, at 10.15 A.M., some glass slides were placed beneath each mushroom. One of the mushrooms was a little further advanced in development than the other. Let us call the more advanced

[1] A large Horse Mushroom (*Psalliota arvensis*) shedding spores in a field during the spore-discharge period is shown semi-diagrammatically in Fig. 76, vol. i, 1909, p. 218.

one A and the less advanced one B. Already by 11 A.M. the mushroom A had produced a good spore-deposit on the slides, whilst B had produced a distinct but relatively poor one. It was clear that spore-discharge had already begun : possibly it had been in progress in A for two hours, but in B probably for only about half an hour. The glass slides were removed and replaced by new ones : and during the whole period of spore-discharge this process of periodical replacement was continued. Usually the slides were changed twice a day, at about 10 A.M. and 8 P.M. respectively. The continuance and vigour of spore-discharge were judged by the eye from the density of the spore-deposits as seen against a background of white paper. In order not to disturb the orientation of the gills, the pots containing the mushrooms were not moved during the whole period of observation.

By making observations in the manner just described, it was found that the mushroom A yielded strong spore-deposits for four days and four nights. The spore-deposit made during the next 24 hours was only very thin, and at the end of this time the fruit-body toppled over and collapsed. The mushroom B yielded excellent spore-deposits for five days and five nights. During the next day and night the spore-deposit was very thin and, toward the end of this time, the mushroom fell over somewhat on its side. Spores then ceased to be liberated, whereupon the mushroom soon collapsed and became putrescent.

From the above observations we may conclude that the spore-discharge period of a wild mushroom is five or six days in length, each day being reckoned as 24 hours. Doubtless, in nature, the period is affected by weather conditions such as temperature and moisture ; but, so far, I have not found it possible to investigate their influence.

At the moment when spore-discharge began, the pilei were convex, but by the second day they had already become flattened. The spores were therefore being shed whilst the gills were being raised into their upward-inclined positions. This movement, as we have seen, does not affect the verticality of the median planes of the gills or prevent the hymenium from continuing to look more or less downwards toward the earth. The discharge of the spores

during the expansion of the pileus was therefore taking place without any spores being wasted by lodging on the gill-sides.

The gills, when spore-discharge began, were pinkish, but by the second day were brown. The brown rapidly deepened so that the gills became almost black. The darkening of the gills, as has already been pointed out, is simply due to the deepening of the pigmented cell-sap in the cells of the gills and is not due to decay or, in the main, to the accumulation of waste spores. Even when the gills had become dark chocolate-brown, the hymenium still continued to liberate vast numbers of spores.

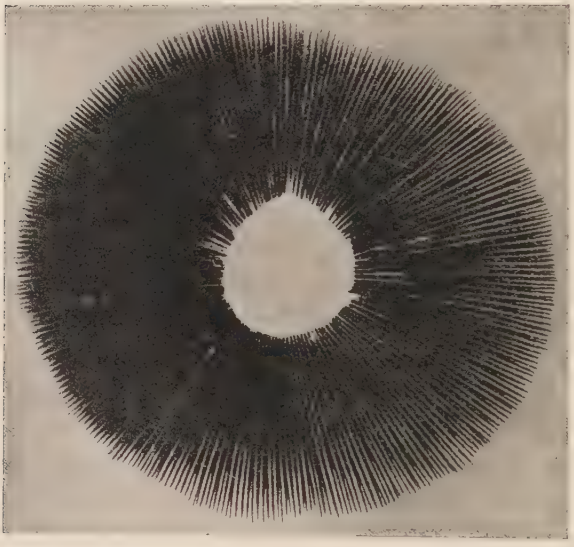


Fig. 141.—A spore-deposit of a wild Mushroom, *Psalliota campestris*, gathered at King's Heath, England. The pileus was placed on white paper for about six hours. To the right, the black spore-lines were formed under interlamellar spaces, while the white spore-free lines were left under the free gill-edges. To the left, the clouding is due to the fact that the gills in this region did not at first look vertically downwards. Natural size.

The number of spores which a mushroom produces can be determined directly, by estimating the number of spores in the spore-deposit (Fig. 141) or, indirectly, by estimating the number of basidia which are formed in the hymenium. A spore-deposit, which had been produced by a wild mushroom within forty-eight hours from a pileus 8 cm. wide, was investigated with a counting apparatus. The result was given in Volume I.[1] The number of spores was found to be 1,800,000,000, from which it was concluded that, on the average, about 40,000,000 had fallen during each hour of the spore-fall period. However, since it has now been shown

[1] Vol. i, 1909, p. 82.

that the spore-discharge period is more than double forty-eight hours, we must conclude that the number 1,800,000,000 was much less than the total number of spores which would have been liberated, had the pileus not been cut off from its stipe but allowed to continue its development to the point of exhaustion in nature.

The number of spores which a mushroom can produce was found by counting the basidia in the following manner. A gill of a wild mushroom, which had been shedding spores for about two days and one night, was removed from the pileus and treated with chlor-zinc iodine. The reagent killed the hymenial cells, but all those basidia which were developing or were soon to develop spores were stained a decided yellow, owing to the presence in them of accumulated protoplasm containing proteins. The yellow basidia on an area of the hymenium measuring forty-nine ten-thousandths of a square mm. were all sketched on paper with the help of a *camera lucida* and were found to number 108. By filling up the spaces in the area and thus allowing for the exhausted basidia which had already shed spores during the period of about two days and one night already mentioned, the number of basidia for the area was increased to 164. The increase allowed for four generations of basidia, fourteen to a generation on the area under investigation, the number 14 being the same as that found by actual observation of similar areas of the living hymenium on other gills of the same fruit-body. The number of generations belonging to the past-generation basidia was taken as four, this being the number which could shed their spores successively in 36 hours if each generation took about 8 hours and 30 minutes for its full development.[1] If we suppose, therefore, that the total number of basidia on forty-nine ten-thousandths of a square mm. is 164, then on one square mm. there would be 33,265 basidia, and these would produce 133,060 spores. The number of spores produced by a square inch of hymenial surface would be 83,162,500 approximately. Now a mushroom about three and three-quarters of an inch in diameter was found to have a hymenial area of 195 square inches. Supposing the packing of the basidia per square

[1] *Vide* Chapter II.

inch to be what we have calculated, this particular mushroom must have produced a total of 18,218,687,000 spores.

As a result of the investigation just described, it may be stated in round figures that a wild mushroom, with a pileus about 4 inches in diameter, possesses a hymenial area of about 1·33 square feet, which contains about 4,000,000,000 basidia which discharge about 16,000,000,000 spores. There can be no doubt whatever that every large wild mushroom which develops in a normal manner liberates upwards of 10,000,000,000 spores.

The Mushroom and the Panaeolus Sub-type.—The gills of *Psalliota campestris* possess all the general characters which have been described for the Aequi-hymeniiferous Type of organisation: the gills are wedge-shaped in cross-section and positively geotropic, the hymenium everywhere looks more or less downwards toward the earth, and every small part of the hymenium (every square mm.) produces and liberates spores during the whole period of spore-discharge. The gills also exhibit all the characters which have been enumerated for the Panaeolus Sub-type, as is indicated superficially by the mottling of the hymenium, which differs in no essential point from that of *Panaeolus campanulatus* or *Stropharia semiglobata*.

Text-book Illustrations of the Hymenium.—For several decades Sachs' figure of a cross-section through the gill of a Mushroom has been considered sufficient by many text-book writers as an illustration for the hymenium of the Hymenomycetes in general. It has been copied from book to book and is familiar to every botanist. Sometimes it has been plagiarised, but slight alterations for the worse do not always prevent one from detecting its original source. Sachs' figure has done excellent service: it has enabled students to realise at a glance some of the main facts in gill-structure; it teaches that the hymenium, subhymenium, and trama are differentiated from one another, and that in any section through the hymenium two kinds of elements may be distinguished, namely, those which bear spores and those which do not; and, finally, it represents fairly correctly the shapes of the various cells, more especially those of the basidia with their club-shaped bodies, their sterigmata, and their oval spores. However, when one comes to

examine the figure and its description in detail, a number of unsatisfactory features soon make themselves apparent. It is stated that "many of the tubes (hymenial elements) are sterile and are called *paraphyses*, others produce the spores and are the *basidia*." [1] In the illustration, four basidia are shown in various stages of development, all protruding beyond the much more numerous sterile cells and all provided with sterigmata. There is nothing in the description of the figure or in the figure itself to indicate whether or not any or all of the sterile elements eventually develop into basidia. So far as my experience goes, the student usually infers that the so-called paraphyses are destined to remain barren, and so comes to the incorrect conclusion that the paraphyses are much more numerous than the basidia. The basidium which has discharged its spores is represented as protuberant; but, as a matter of fact, a basidium at such a stage in its history rapidly collapses and sinks down to the level of the paraphyses. Collapsed basidia are entirely unrepresented. There is nothing in the illustration to indicate that the whole number of basidia develop in an orderly series of successive generations. The hymenium is not nearly so sharply differentiated from the subhymenium as is shown, but the one passes gradually into the other. Finally, no surface view of the hymenium accompanies the cross-section, so that it is impossible to obtain more than a very limited idea of the organisation of the hymenium as a whole. These criticisms of Sachs' illustration of the hymenium of *Psalliota campestris* apply equally to Strasburger's illustration for *Russula rubra*.[2]

Van Tieghem [3] reproduces Sachs' figure of the hymenium and states that the shorter elements (those not bearing sterigmata) remain sterile and are the paraphyses, whilst the other longer elements which project above the general level of the hymenium (all of which in the illustration have sterigmata) are the basidia. This, as we shall see, is an erroneous division of the elements, for many of the shorter ones are certainly young basidia.

[1] K. Goebel, *Outlines of Classification*, etc. A new edition of Sachs' *Text-book of Botany*, Book II, English translation, Oxford, 1887, p. 134.

[2] Strasburger, Schenck, Noll, and Karsten, *A Text-book of Botany*, third English (based on eighth German) edition, London, 1908, p. 408.

[3] Van Tieghem, *Traité de Botanique*, Paris, 1884, p. 1049.

I shall now endeavour to explain the organisation of the hymenium of the Mushroom in detail, and the reader will find that it is essentially the same as that of *Panaeolus campanulatus* and *Stropharia semiglobata*. However, the hymenial elements of the Mushroom are very much smaller than those of these two species, and their investigation has therefore been proportionally more difficult to carry out.

The Mottling of the Gill Surface.—The hymenium covering the exterior of each gill which has become outstretched is finally mottled with small lighter and darker areas (Fig. 134, B, p. 377). The pattern is similar to that already described for *Panaeolus campanulatus* and *Stropharia semiglobata*, but finer. This relative fineness is in part due to the fact that the diameter of the basidium of a Mushroom is only about one-half that of the basidium in the other species. If a dark area of a Wild Mushroom be examined with the microscope, it is found to possess a large number of basidia, each of which is bearing four spores which have already become pigmented. The darkness is simply due to the colour of the spores. The light areas, on the other hand, contain basidia which are just about to develop spores or which bear spores which may or may not have attained full size but are still unpigmented. The relative lightness is due to the absence of spore-wall pigment.

With the help of the microscope, one finds that the light and the dark areas are irregularly shaped and very variously arranged in respect to one another. A semi-diagrammatic drawing of the hymenium of a Cultivated Mushroom, in which are shown only the spores and the basidia which have produced them, is reproduced in Fig. 142. Here we see a light area surrounded by a dark area. The dotted contour-line indicates the limits of the former, while the arrows point to the directions in which the line is being pushed. Just outside the line, the spores on the dark area are being gradually discharged, while just inside it new basidia are coming to maturity and producing spores, so that as the dark area becomes reduced the light area becomes extended. There are such waves of development passing over the hymenium in a very irregular manner in all directions on every gill. In the course of a few hours, every dark area, owing to the discharge of its spores,

becomes a light area, and every light area, owing to the development upon it of spores which have become pigmented, becomes a dark area. A single area becomes alternately dark and light a

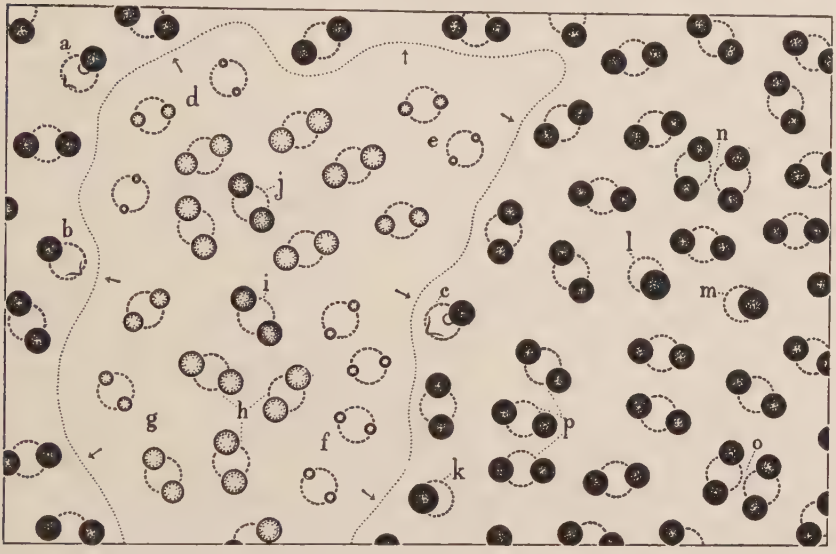


Fig. 142.—*Psalliota campestris* (cultivated form). Surface view of a piece of hymenium 0·15 mm. long and 0·1 mm. wide, semi-diagrammatically showing a white area surrounded by a dark area. The spores alone have been fully sketched, but the positions of the spore-bearing basidia are indicated by dotted circles. The white area is enlarging at the expense of the dark area: the dotted line indicates the limits of the white area and the arrows the directions of its extension. The basidia at *a*, *b*, and *c*, just outside the dotted ring, have each discharged one of their two spores; and at *a* and *c* water-drops are being excreted at the bases of the remaining spores in preparation for spore-discharge. The basidia at *d*, *e*, *f*, and *g* in the white area are developing spores which as yet are only from 3 to 15 minutes old but which are rapidly attaining full size. At *h* the spores are older and of full size but colourless. At *i* and *j* the spores are still older and are becoming pigmented. At *k*, *l*, and *m* in the dark area the basidia have developed only one spore each, but the spore has twice the normal volume. At *n* and *o* two adjacent basidia have developed spores simultaneously and the four spores in each group have arranged themselves so that they occupy the corners of a square. At *p*, also, the spores are so arranged that those of adjacent basidia can not come into contact during development or discharge. Magnification, 706.

number of times in succession during the several days of the spore-discharge period. The actual passage of slow waves of development over the hymenium of a Cultivated Mushroom was witnessed for a gill kept under continuous observation for eight hours in a compressor cell in the manner described in Chapter II.

Whilst the spores on an originally light area are in the early stages of pigmentation, the tint of the area is intermediate between that of a light and that of a dark area. If we wish, therefore, we can speak of three different kinds of areas as making up the mottled hymenial pattern: dark, light, and intermediate. With the microscope it is not difficult to detect intermediate areas here and there: they often mark the transition of a light area into an adjacent dark one. If the reader desires any further details in regard to the general phenomenon of mottling, he should turn to the fuller account given in the description of the organisation of *Panaeolus campanulatus*.[1]

Methods for Examining the Hymenium in Surface View.—The method described in Chapter II was made use of for the purpose of examining a large area of the hymenium with the low power of the microscope (magnification about 130), *i.e.* a living gill was mounted on a tiny drop of water in a compressor cell. However, owing to the small size of the basidia and spores, it was found necessary to magnify the hymenium with the high powers of the microscope. Now the gills are pigmented and absorb much of the light passing through them. Therefore, in order to increase the amount of light striking the hymenium when viewed with high powers, the following procedure was adopted. A gill was dissected away from a living fruit-body, wrapped around a finger, and from it a very thin surface-section was taken with the help of a hand-razor. A small drop of water was placed on a glass slide. The section was then mounted on the drop, so that its under sub-hymenial side alone was wetted, and then covered with a cover-glass. The result of these operations was that a thin and fairly transparent section was obtained which could not dry up quickly and which possessed a hymenium which looked upwards under a cover-glass without being wetted. The cover-glass only touched and injured certain parts of the section, so that a sufficient amount of the hymenium was left for examination in the normal condition. Strong daylight was directed through the preparation from the mirror.

The Number and Size of the Spores on Individual Basidia.—The

[1] Chapter X.

number of spores on individual basidia was determined by the method just described, *i.e.* by the examination of the living hymenium in surface section. It was found that this number is not identical for Wild and Cultivated Mushrooms.

In Wild Mushrooms gathered in several places in England (Birmingham, Redditch, etc.) the number of spores on each basidium

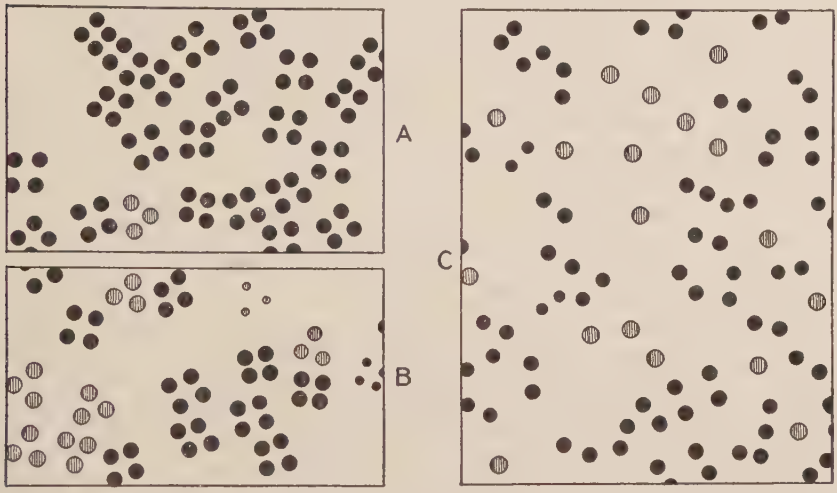


FIG. 143.—*Psalliota campestris*. *Camera-lucida* drawings of the spores of the present-generation basidia on the living hymenium. A and B, from a wild form of the fungus; C, from a cultivated form. In A, the basidia are tetrasporous with one exception which is trisporous. In B, in addition to the tetrasporous basidia, there are a number of trisporous basidia. The spores of the tetrasporous basidia are shown black, whilst those of the trisporous are shaded with lines. In C, most of the basidia are bisporous, but others are monosporous. The spores of the bisporous basidia are shown black, whilst those of the monosporous are shaded with lines. Magnification, 440.

was usually four; but here and there on the hymenium, mixed with these quadrisporous basidia, were frequently found a certain number of trisporous basidia which occurred either singly or in little groups. In Fig. 143, A, is shown a small area of the hymenium in which only one trisporous basidium is associated with the normal quadrisporous basidia, while at B is shown another similar area in which trisporous basidia are almost as numerous as the quadrisporous. In these drawings, all the groups of four spores have been represented in uniform black, whilst the groups of three spores, for the sake of distinction, have been shaded with straight lines;

but, in actual fruit-bodies, the colour of the spores is not in the least dependent on the number of spores produced per basidium, but only on the degree of spore-maturity.

In a variety of Cultivated Mushroom, which I grew on a bed of horse manure at Birmingham, England, the basidia were found to be usually bisporous; but, mixed with the bisporous basidia, were a larger or smaller number of monosporous basidia. An area of the hymenium showing spores in pairs (represented in uniform black) and single spores (shaded with lines) is illustrated in Fig. 143, C. Bisporous basidia, as well as a few monosporous basidia, are also shown in Fig. 142 (p. 407).

In no fruit-body of the Wild Mushroom could I find a basidium with either one or two spores upon it; and, corresponding with this, in no fruit-body of the Cultivated Mushroom could I find a basidium with either three or four spores on it. However, it would not be a matter of surprise to me if varieties of Mushrooms were discovered in which monosporous, bisporous, trisporous, and quadrisporous basidia occurred mixed together on the same hymenium.

It was pointed out in the first volume of this work that both Atkinson and I have found two-spored varieties of Mushrooms coming up upon the campus of our respective Universities.[1] It is therefore possible that, in North America at least, there is a Wild Mushroom with two-spored basidia; but, to obtain certainty in this matter, further observations are necessary. It seems very likely that the two-spored varieties of *Psalliota campestris* have been derived by mutation from the four-spored.[2]

In regard to the size of the spores, it is to be noted that the spores on a trisporous basidium in a Wild Mushroom are slightly larger than those on a quadrisporous basidium (Fig. 143, A and B, p. 409), and also that the spore on a monosporous basidium in a Cultivated Mushroom is distinctly larger than the spores on a bisporous basidium (Fig. 143, C). In giving the average size of the spores, this fact ought to be taken into account. Usually, in a spore-deposit from a Cultivated Mushroom, one can distinguish by their size with a fair amount of certainty which spores have

[1] Vol. i, 1909, p. 15. [2] *Ibid.*

come from monosporous basidia and which from bisporous basidia. If one were to plot out a curve showing the variations in size of a large number of spores of a single Cultivated Mushroom, one would find that the curve would have two peaks.

In a Cultivated Mushroom, the spores of the monosporous basidia have a volume of about twice that of the spores of the bisporous basidia. This is associated with the following facts. The basidium-bodies of the monosporous and bisporous basidia are equal in size (*vide infra*, Fig. 147) and, before the formation of the spores, are equally filled with protoplasm. This protoplasm is eventually all poured into the spores (with the probable exception of a very thin lining layer), and the spores become stuffed with it. Where there are two spores on the basidium, the protoplasm is equally divided and, where there is only one, it is undivided. The volumes of the spores on the monosporous and bisporous basidia are correlated with the relative amounts of protoplasm which the spores are destined to contain.

It seems very probable that the behaviour of the nuclei is different for monosporous and bisporous basidia on the same hymenium of a Cultivated Mushroom, and different also for the trisporous and quadrisporous basidia of a Wild Mushroom. This is a matter which invites cytological investigation.

The complete emptying of the contents of a basidium-body (with the probable exception of a very thin lining layer necessary for maintaining turgidity) into the spores, whilst these are ripening, is a phenomenon which occurs not merely in *Psalliota campestris* but quite generally in Basidiomycetes. I have observed it in a large number of species. If, therefore, one finds a spore-bearing basidium only partially empty, one may be quite sure that the spores, although of full size and partially or completely pigmented, are not yet fully ripe, and that a stream of protoplasm is still passing into them through the fine necks of the sterigmata. This is a fact that ought to be borne in mind by all cytologists when studying nuclear behaviour in connection with basidia.[1]

It has been shown that the relative size of the spores of monosporous and bisporous basidia in a Cultivated Mushroom is directly

[1] *Cf.* Chap. I, pp. 27–29.

correlated with the amount of nutrient protoplasm which each kind of spore is to receive. This conclusion suggests another of a more general kind, namely, that the fluctuating variations in the size of the spores for any species belonging to the Hymenomycetes are correlated with the amounts of protoplasm in the basidia which produce the spores. Now the amounts of protoplasm in the basidia usually vary directly as the volume of the basidia. It therefore seems highly probable that, if of two individual fruit-bodies of the same species one has spores which on the average are larger than those of the other, the one with the larger spores will have the larger basidia. Spore-size is not improbably correlated with corresponding variations in size in all the elements of the hymenium, and perhaps of all the elements of the whole fruit-body. In studying a large number of species of the genus Coprinus, I have found that the species with the largest spores have the largest basidia, and those with the smallest spores the smallest basidia. So far as species of Coprinus are concerned, there is undoubtedly a strict correlation between spore-size and basidium-size.

Rate and Mode of Development of the Spores of an Individual Basidium.—The rate of development of the four spores of a single basidium from their first rudiments up to full size was determined by direct observations made upon a Wild Mushroom gathered in England. A gill was dissected off the fruit-body and placed on a glass slide, and over it was laid a large cover-glass. No mounting fluid was employed; but, on the autumn day when the investigation was undertaken, the air was almost saturated with moisture, so that the gill under the cover-glass lost water but very slowly indeed. Two basidia, one with fully pigmented nearly ripe spores belonging to an older generation, and another which had developed sterigmata but not spores and belonged to a younger generation, were watched, and sketches of them were made at intervals. The first beginnings of the new spores on the sterigmata of the younger basidium are shown in Fig. 144 at A. After an interval of 10 minutes from the beginning of the observations, the spores had grown to half their full diameter (B), after 20 minutes to about three-quarters (C), and at the end of 30 minutes they had attained

their full size (D). A similar set of sketches, made in succession with 10-minute intervals, is shown in Fig. 145. In this instance, the spores of both the younger basidia attained to their full size

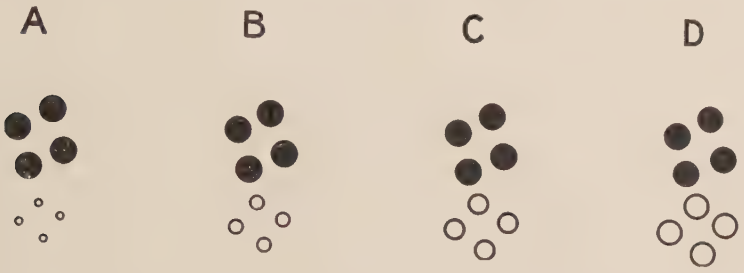


FIG. 144.—*Psalliota campestris*, wild form. Rate of growth of spores on the ends of the sterigmata. A, the spores of two basidia, one set full-grown and the other just coming into existence, as seen on a living gill. B, C, and D, sketches of the same made successively with intervals of 10 minutes. The spores attained full size in about 30 minutes. Magnification, 820.

within 40 minutes. We may conclude, therefore, that the spores of a Wild Mushroom at room temperatures take only from 30 to 40 minutes to grow to full size.

In order to observe the course of the development of the spores after they have attained full size, it was found necessary to resort

FIG. 145.—*Psalliota campestris*, wild form. Rate of growth of spores on the ends of the sterigmata. A, the spores of four basidia, two sets full-grown and two just coming into existence, as seen on a living gill. B, C, D, and E, sketches of the same made successively at 10, 20, 30, and 40 minutes respectively after the stage A. The young spores attained full size in a little less than 40 minutes. Magnification, 296.

to the compressor-cell method. A piece of a gill was taken from a Cultivated Mushroom and placed on a very small water-drop in a compressor cell. The lid of the cell was then closed down, so that it just touched the gill at one spot. It thus became possible to observe the hymenium with a magnification of about 300 diameters. By using this method it was observed that the

spores, after attaining full size, remained colourless for about two hours. Then the process of pigmentation of the spore-walls set in, and the walls continued to deepen in colour for about two hours. After pigmentation of the spores had been completed, the spores remained on the ends of their sterigmata for about three hours and ten minutes. At the end of this time they were shot away. The time taken by a spore to develop from a tiny rudiment on the end of its sterigma up to maturity and ultimate discharge was approximately eight hours.[1]

An Analysis of the Hymenium of the Cultivated Mushroom.—The analysis of the hymenium about to be given is similar to that for *Panaeolus campanulatus.*

Any small portion of the hymenium, such as that which is included within a dark or a light area of a gill and which has begun to shed spores, is made up of the following elements :

1. Past-generations Basidia,
2. Present-generation Basidia,
3. Coming-generation Basidia,
4. Future-generations Basidia, and
5. Paraphyses.

On any small portion of the hymenium the basidia come to maturity in a series of successive generations, and the paraphyses—the permanently sterile elements—undergo gradual enlargement during the progressive exhaustion of the basidia in exactly the same manner as has been already described for *Panaeolus campanulatus.*

The arrangement of the various elements of the hymenium in respect to one another in surface view is shown semi-diagrammatically in Fig. 146. On account of the small size of the basidia and paraphyses and the consequent increase in the optical difficulties of investigation, it was not found possible to make *camera-lucida* drawings showing the positions of all the elements in an actual surface view of the hymenium. Fig. 146, however, gives a synthesis of a number of detailed observations and is sufficiently correct. It will be found to agree in all

[1] *Cf.* Chap. II.

essentials with similar Figures for *Panaeolus campanulatus* and *Stropharia semiglobata*, which were actually made with the help of the *camera lucida*.

The area of Fig. 146 is approximately equal to one-hundredth of a square mm. The present-generation basidia (those bearing spores) are identical with those shown in the right two-thirds of Fig. 142 (p. 407). The piece of hymenium is supposed to have been shedding spores for about 24 hours, so that already it contains a number of basidia belonging to past generations. However, it is far from exhaustion. Indeed, it should continue to shed spores for at least four days longer. New generations of spores are potentially resident in the coming-generation basidia and in the numerous basidia belonging to future generations. There are no cystidia on the surface of the gills. All the elements belong to one or other of the following five groups : past-generations basidia, *a a* ; present-generation basidia, *b b* ; coming-generation basidia, *c c* ; future-generations basidia, *d d* ; permanently sterile paraphyses, *e e*.

The past-generations basidia, *a a*, are collapsed and shrunken, devoid of protoplasmic contents, with tops drawn down to the general level of the hymenium. Their free ends are concave and contain the remains of the sterigmata which are reduced to mere stumps. When a mushroom has been shedding spores for five or six days and is in the last stages of hymenial exhaustion, most of the past-generations basidia are found to have entirely disappeared. No such disappearance of these elements, however, is shown in the present drawing, as the piece of hymenium is supposed to have been shedding spores for not more than 24 hours.

The present-generation basidia, *b b*, are distinguished from all others by the fact that they bear spores. The spores on the left-hand side of the Figure are colourless and many of them have not attained full size, while those on the right-hand side are of full size and completely pigmented. Most of the basidia of the present generation are bisporous, *b b* ; but here and there certain of them are monosporous, *m m*. The spores on the latter have decidedly larger diameters than those on the former. As soon as a present-generation basidium has shed the last of its spores, it becomes a past-generation basidium : after about twenty

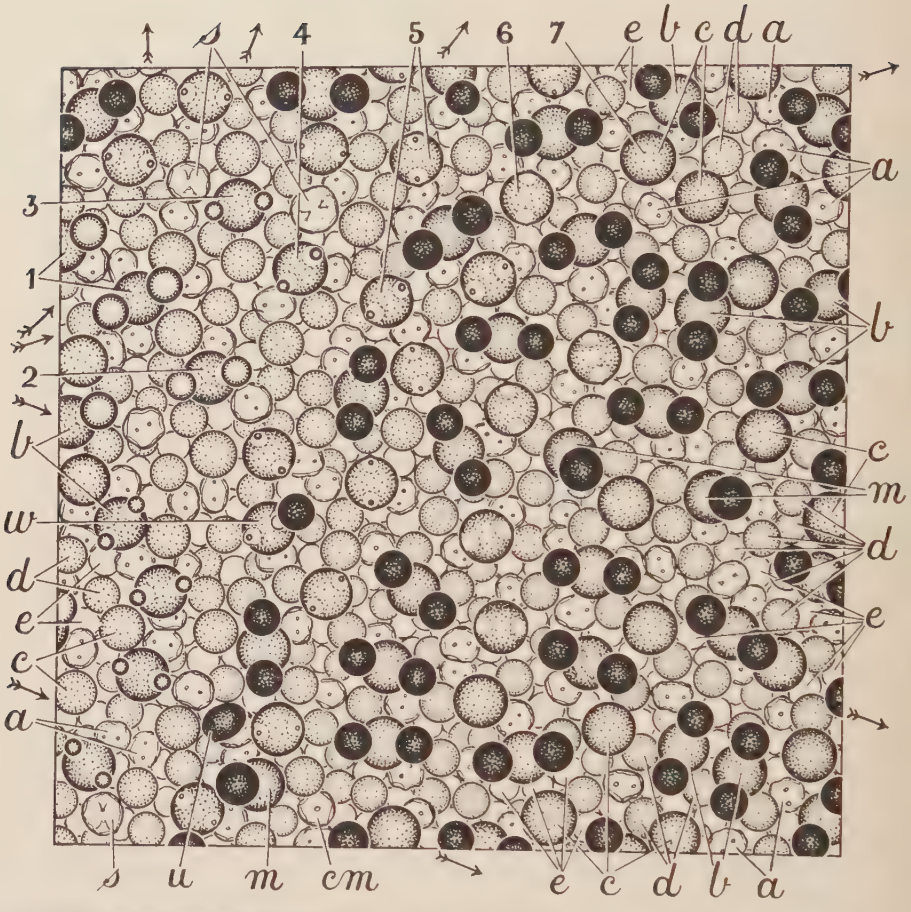


FIG. 146.—*Psalliota campestris* (cultivated form). Semi-diagrammatic surface view of the living hymenium of a Mushroom, about 24 hours after the beginning of the spore-discharge period. The length of each side of the square is 0·1 mm., so that the area of the square is equal to 0·01 of a square mm. All the elements belong to one or other of the following five groups: past-generation basidia, *a a*; present-generation basidia, *b b*; coming-generation basidia, *c c*; future-generation basidia, *d d*; permanently sterile paraphyses, *e e*. A wave of development is proceeding from the light area on the left to the dark area on the right in the directions shown by the arrows. The series 1 to 7 are basidia in successively younger stages of development. No. 1, basidia with spores which are full-sized but young (only about 1 hour old) and unpigmented; no. 2, basidium with spores not yet of full size (about 30 minutes old); no. 3, basidium with spores only one-third of their eventual diameter (about 10 minutes old); no. 4, basidium with spores which have just begun their existence (about 5 minutes old); no. 5, basidia with sterigmata fully developed but no spores; no. 6, basidium with sterigmata just beginning to develop; no. 7, basidium as yet without even a trace of sterigmata. Nos. 1 to 4 belong to the present-generation basidia of the light area, while nos. 5 to 7 belong to the coming-generation basidia of the dark area. Spore-discharge is taking place at the left-hand side of the dark area. The basidia *s s* have just discharged their spores and are collapsing; their sterigmata are sinking into a concavity which is forming at the end of each basidium-body. The basidium *w* is just discharging the second of its two spores and, as a preliminary thereto, a drop of water has been exereted within the last 10 seconds at the spore-hilum. Most of the basidia of the present generation are bisporous, *b b*; but, here and there, certain basidia are monosporous, *m m*, and have larger spores. A past-generation basidium, if it has two sterigmatic stumps, has been derived from a bisporous basidium; but, if it has only one such stump, as shown at *cm*, it has been derived from a monosporous basidium. An undischarged or waste spore lying on its side and adherent to the surface of the hymenium is shown at *u*. (The present-generation basidia are identical with those shown in the right two-thirds of Fig. 142.) Magnification, 1,060.

minutes it collapses, its end becomes concave, and it is drawn down to the general level of the hymenium. A past-generation basidium which has two sterigmatic stumps in its concave end has been derived from a basidium that was bisporous; but one which has only one such stump, as shown at *cm*, has been derived from a monosporous basidium, such as *m m*. The basidium-body of each present-generation basidium is shaped more or less like a club with the swollen end directed outwards. This swollen end protrudes slightly above the general level of the hymenium and therefore hides to a greater or less extent the immediately adjacent past-generations basidia, future-generations basidia, and paraphyses. Owing to this fact, the optical difficulties in making out the structure of the hymenium in surface view are considerably increased. The amount of massive protoplasm inside the body of a present-generation basidium, *i.e.* all the protoplasm except a very thin layer lining the walls which probably remains until the basidium collapses and dies, varies greatly in correspondence with the age of the spores. When the spores are just beginning their development on the ends of the sterigmata and are the merest rudiments, the basidium-body and sterigmata are filled or almost completely filled with protoplasm; but, as the spores grow in size and for several hours after they have attained their full size, and even whilst they are undergoing pigmentation, the protoplasm flows through the sterigmata sporewards. This progressive evacuation of the basidium-body continues until the spores are ripe and ready to be discharged, and it is only then that the basidium-body and sterigmata appear transparent and empty of solid contents. As the massive protoplasm moves out of the basidium, its place is taken by cell-sap.

The coming-generation basidia, *c c*, are the basidia which are destined to produce a new crop of spores as soon as the crop upon the present-generation basidia has been discharged and the basidium-bodies of these elements have collapsed and sunk down to the general level of the hymenium. As soon as the present-generation basidia begin to develop spores, certain other basidia in their immediate vicinity become clearly marked out as their successors, *i.e.* as the coming-generation basidia, by their rapidly increasing size and prominence, and by the fact that they are

filled with dense protoplasmic contents. The development, ripening, and discharge of the spores of the present-generation basidia, as we have seen, take about eight hours to accomplish. During this time, the coming-generation basidia interspersed between them are by no means quiescent. They first complete the growth in length and diameter of their basidium-bodies, so that these become equal to those of the present-generation basidia (*cf.* *b* and *c*, on the right-hand side of Fig. 146). Then the fusion-nucleus in each basidium divides and so produces nuclei which are subsequently to be translated to the spores. I have not attempted to study the nuclear divisions in the basidium, and therefore am unable to state from my own observations whether the fusion-nucleus divides into two or four nuclei. However, René Maire, who made a cytological investigation upon the bisporous basidia of a Cultivated Mushroom, states : that there are two nuclei in the young basidium which unite to form a fusion-nucleus (secondary nucleus) ; that this nucleus then behaves in the usual manner, *i.e.* it produces four nuclei by two successive divisions—a process probably accompanied by the reduction of the chromosomes to one-half [1] ; and that, after the first of these nuclear divisions has taken place, the basidium begins to produce its two sterigmata.[2] The development of the sterigmata is a slow process which requires at least thirty minutes. Usually a coming-generation basidium begins to develop its sterigmata about half an hour or so before the moment when the nearest present-generation basidium will discharge its last spore. Thus the sterigmata of the coming-generation basidia are almost ready (within 15 minutes or so of being ready) to develop spores at the moment when the hymenium in their immediate neighbourhood has become cleared of the spores of the previous generation of basidia. Thus one crop of spores is quickly followed by another. It is in consequence of this very orderly mode of development of one generation of basidia after another that by far the greater part of the hymenium at any moment is found to contain spore-bearing basidia. As soon as a basidium begins to develop the

[1] René Maire, "Recherches cytologiques et taxonomiques sur les Basidiomycètes," *Bull. Soc. Myc. France*, T. 18, 1902, p. 151.

[2] *Ibid.*, p. 152.

rudiments of spores on the tips of its sterigmata, it must be considered to have passed from the coming to the present generation. The number and general distribution of the basidia of a coming generation on any given area of the hymenium are equal to those of the present generation, and it is a general rule for any generation of basidia that each basidium in it shall be sufficiently well separated from its neighbours to enable it to develop and discharge its spores without being jostled.

We have seen that, according to René Maire, four nuclei are produced in the body of a coming-generation basidium as a result of two divisions of the fusion-nucleus. According to this author, two of the nuclei pass up one sterigma into one spore and two pass up the other sterigma into the other spore. Then each nucleus divides, so that each ripe spore comes to contain four nuclei. Maire noticed, however, that sometimes the fusion-nucleus only divides once, and then, he says, each spore only receives one nucleus, which afterwards may divide once or twice.[1] He does not appear to have observed that monosporous basidia frequently occur in the hymenium of the Cultivated Mushroom. It seems to me that further investigation is required to clear up the irregularity to which Maire refers. It may be that, when the fusion-nucleus only divides once, a single sterigma and spore are produced and not two ; whereas, when there are two divisions, there may always be two sterigmata and two spores formed. In any case, cytologists, when studying the Cultivated Mushroom, must in future take into account the fact that there are two kinds of basidia present in the hymenium—bisporous and monosporous.

One of the most remarkable events in the development of a basidium in the Hymenomycetes generally is the migration of the four nuclei from the basidium-body into the spores through the four extremely narrow sterigmatic necks. This has been studied cytologically by Ruhland,[2] Maire,[3] Fries,[4] and more recently by

[1] René Maire, *loc. cit.*, p. 152.

[2] W. Ruhland, "Zur Kenntnis der intracellularen Karyogamie bei den Basidiomyceten," *Bot. Zeit.*, Jahrg. 59, 1901, Abt. I, pp. 187–206.

[3] René Maire, *loc. cit.*

[4] R. E. Fries, "Zur Kenntnis der Cytologie von *Hygrophorus conicus*," *Svensk. Bot. Tidskrift*, vol. 5, pp. 241–251.

Levine.[1] The first of these observers showed that, when traversing a sterigmatic neck, a nucleus undergoes a great alteration in shape : it becomes drawn out into a filament. The other workers have observed fibrillar strands leading upwards from the nuclei into the sterigmata and sometimes into the spores. According to Levine, at the end of the second nuclear division in the basidium-body, the four centrosomes become attached to the free end of the wall of the basidium and the four daughter nuclei become reconstructed in close connection with them. The four nuclei then move downwards somewhat in the basidium but maintain their connections with the centrosomes by means of fibrillar strands. The positions which the centrosomes take up at the free end of the basidium-wall mark the points of origin of the sterigmata ; and, as these structures develop, the centrosomes are carried up in their tops. The fibrillar strand connecting each nucleus with its centrosome becomes elongated during this process. When the spores begin to be formed on the ends of the sterigmata, the centrosomes still remain attached to the cell-wall and come to occupy positions destined to be the spore-apices. Each fibrillar strand again elongates during the growth of the corresponding spore to full size, so that eventually the four nuclei which may be situated some distance down the basidium-body, are attached by relatively very long and thin fibrillar strands with the centrosomes at the apices of the spores.[2] Maire, Fries, and Levine all agree that the fibrillar strands are associated in some way with the passage of the nuclei into the spores. The strands occupy the paths of the nuclei and possibly direct the nuclear migrations. Levine says that, since the strands pass not merely through the sterigmata but also into the spores, they may be of significance in the apparently difficult process of passing the nuclei through the extremely narrow sterigmatic necks. I am inclined to agree with this view. It remains, however, to be discovered whether the strands are kinoplasmic and contract, so that they drag the nuclei into the spores, or whether they merely represent lines of

[1] M. Levine, "Studies in the Cytology of the Hymenomycetes, especially the Boleti," *Bull. Torrey Botanical Club*, vol. xl, 1913, p. 173.

[2] M. Levine, *loc. cit.*, pp. 172–173.

least resistance of which each nucleus can take advantage during its migration.

In the Wild Mushroom, where most of the basidia are quadrisporous, the passage of the four nuclei into the four spores probably takes place in the typical manner described above. In the Cultivated Mushroom, according to Maire, two nuclei travel up each of the two sterigmata into the two spores. Further investigation is required to determine whether the tip of each of the two sterigmata contains two centrosomes instead of the normal one, and whether or not, just before the nuclear migrations, there are two fibrillar strands running through each sterigma, each strand connecting a nucleus with the apex of the same spore.

The future-generations basidia, *d d* (Fig. 146, p. 416), are distinguished from the present-generation basidia by not bearing sterigmata or spores, and from the coming-generation basidia by their relatively small size and by the fact that they are not yet protuberant. They are usually filled or nearly filled with fine protoplasm, and their basidium-bodies, which are always shorter than those of the present-generation and coming-generation basidia, are relatively transparent. It is possible that the two nuclei with which each of these basidia is provided at its origin have not as yet fused, but this point awaits decision by means of a direct investigation. The future-generations basidia vary somewhat in size, and one is led to suspect that eventually the larger ones produce spores before the smaller. In the piece of hymenium represented in Fig. 146, the future-generations basidia are more numerous than those of any other class. This is associated with the fact that the hymenium is still young (it is supposed to have been shedding spores for only about 24 hours). The future-generations basidia will develop spores during the next three or four days of the spore-discharge period, at the end of which time they will all have become past-generations basidia. It is probable that the total number of generations of basidia produced on any one small area of the hymenium is at least ten.

The paraphyses, *e e* (Fig. 146, p. 416), are numerous small elements which are non-protuberant and largely hidden by the basidia, especially by the swollen ends of the bodies of the

present-generation and coming-generation basidia. It is not easy, at the stage of development of the hymenium represented in Fig. 146, to distinguish the paraphyses from some of the future-generations basidia, but they undoubtedly are present in about the numbers shown. As the hymenium grows older and more and more basidia shed their spores and collapse, the paraphyses increase in diameter ; and then they can be seen more easily. When the hymenium is quite exhausted, the paraphyses alone have a turgid appearance, and are then seen to be very numerous. A mushroom had been shedding spores for six days and six nights. A few hours after the cessation of spore-discharge, one of its gills was carefully examined with the microscope and it was found that nearly all the basidia had completely dissolved, so that their outlines could only be traced here and there ; but the paraphyses could all be clearly distinguished. A surface view of this totally exhausted hymenium is shown in Fig. 152, C (*vide infra*, p. 448).

It has frequently been denied that paraphyses, *i.e.* constantly occurring permanently sterile elements, are present in the hymenium of the Hymenomycetes[1] ; but the denials have been made by cytologists who have been content to examine fixed and stained microtome sections. By comparing the state of the living hymenium of a single fruit-body day after day throughout the whole period of spore-discharge for *Panaeolus campanulatus* and *Stropharia semiglobata*, I proved the existence of paraphyses in those species.[2] A similar investigation upon the Mushroom has yielded a similar result. I cannot entertain any further doubt that the hymenium of *Psalliota campestris* contains numerous paraphyses destined from their first origin to remain sterile. There does not seem to me to be the slightest reason to suppose that these elements could be caused to develop into basidia by any normal variation of any of the natural conditions under which mushrooms grow.

Since paraphyses are definite elements in the hymenium of the Mushroom, one may ask : what is their function ? I am inclined to think that they serve the purpose of assisting the basidia which are to shed spores. They are the elastic elements of the hymenium.

[1] *Cf.* Chap. X, pp. 269–270.

[2] *Vide* Chap. X, pp. 279–281, and Chap. XI, pp. 336–337.

As the hymenium gets older and as more and more basidia shed their spores and collapse, the paraphyses become larger and larger, and so fill up the gaps between the still living basidia. To these they probably minister by giving mechanical support and moisture, and possibly in other as yet unsuspected ways.[1]

In Fig. 146 (p. 416), a wave of development is passing across the hymenium from the left to the right in the directions shown by the arrows. This wave has already been dealt with, so far as the present-generation basidia are concerned, in the section which treats of the mottling of the gills (*cf.* Fig. 142, p. 407, which has the same present-generation basidia in its right two-thirds as Fig. 146). But here all the elements of the hymenium are represented, so that it is now possible to explain the nature of the wave in greater detail. The series of elements nos. 1, 2, 3, 4, 5, 6, and 7 in Fig. 146 are basidia in successively younger stages of development. No. 1 indicates two basidia with full-sized but unpigmented spores. The spores are supposed to be only one hour old, and therefore to have attained their full size only about twenty minutes ago. No. 2 indicates a basidium which bears spores which have not yet attained full size. These spores are only about thirty minutes old. The basidium no. 3 bears spores which have attained only one-third of their eventual diameter and are only about ten minutes old. The basidium no. 4 bears spores which have just begun their existence and are only about five minutes old. No. 5 points to two basidia which possess fully developed sterigmata but no spores. The basidium no. 6 has sterigmata which are just beginning to develop. The basidium no. 7 is as yet without even a trace of sterigmata. Similar series of basidia can be seen anywhere in the Figure passing from left to right in the direction of the arrows. Nos. 1 to 4 belong to the present-generation basidia of the light area, while nos. 5 to 7 belong to the coming generation of the dark area. Spore-discharge is taking place on the left-hand side of the dark area and is proceeding to the right-hand side in the direction of the arrows. The basidia *s s* discharged their spores about twenty minutes ago and are in the act of collapsing: their sterigmata are sinking

[1] *Cf.* Chap. X, pp. 282–283.

into a concavity which is forming at the end of each basidium-body. Soon the sterigmata will melt down to stumps and then these basidia will resemble the other past-generations basidia, *a a*, scattered throughout the Figure. The basidium *w* is just about to discharge the second of its two spores, the first having already been shot away leaving behind a stiff but naked sterigma. As a preliminary to the discharge of the second spore, a drop of water has been excreted at the spore-hilum within the last ten seconds. The drop is almost of maximum size, which fact indicates that the spore should be violently propelled from its sterigma within the next two seconds. The spores on all the other basidia at the extreme left edge of the black area should be shot away within about half an hour. The successive discharge of all the spores on the black area, proceeding from the left to the right of the Figure, might take an hour and a half or two hours. If one could watch the gradual disappearance of the spores in this way, one would perceive that the basidia indicated by the series which bear the numbers 1 to 7 would be continuing their development, so that the area which is now dark would gradually again come to be spore-bearing, proceeding from left to right. Thus, for instance, the basidium no. 6 would be observed to begin developing its spores within a few minutes of the moment of discharge of the last of the six spores on the three present-generation basidia with which it is now surrounded. If we could watch the basidium no. 6 developing its spores, we should find that, during the early stages of its development, the spores on basidia nos. 1 and 2 would undergo pigmentation, those on nos. 3 and 4 would grow to full size, and those on no. 5 would grow to nearly full size. It is thus clear that, as the wave of development passes across the piece of hymenium, a great many basidia are undergoing progressive and synchronous changes, all leading to the climax of spore-discharge. Everywhere throughout the finely mottled surface of the hymenium, on every gill, waves similar to the one just described are moving; but the movements are in various directions. Sometimes a series of waves following one another in regular succession moves over several light and dark areas in a straight line in one direction; but more often the waves clash, move apart from one another, or interfere

with one another in endlessly varied ways. One can find out only empirically the directions of the waves on any gill-surface, and it is impossible to predict their course theoretically. Even the waves which are opposite to one another on the two sides of the same gill go their ways quite independently of one another.

The very numerous small irregular waves of development which we find in all representatives of the Panaeolus Sub-type, including the Mushroom, may be contrasted with the single large wave which, in all species of the genus Coprinus, passes from below upwards on each gill. A black-spored panaeolate fungus with a many-waved hymenium on each gill may well have been the ancestor of the genus Coprinus in which the hymenium on each gill is one-waved, the many small irregular waves having become reduced in the course of evolution to one grand wave always moving in an upward direction.

We shall now proceed to a study of the hymenium of the Cultivated Mushroom in cross-section, so that we may gain an insight into the structure and mutual relations of the hymenial elements when these are seen in lateral view. Fig. 147 represents a cross-section of part of a living gill and shows semi-diagrammatically the structure of the hymenium *h*, the subhymenium *s*, and part of the trama *t*. The drawing is essentially synthetic and exhibits all the histological details which were made out by the study of numerous particular sections cut with a hand-razor from living gills and mounted in water. Parts of some of these sections were drawn with the *camera lucida*. Similar sections for the wild form of the Mushroom will be represented in subsequent illustrations. The gill in Fig. 147 is supposed to be taken from a mushroom which has been shedding spores for about 24 hours and which therefore will continue to shed spores for several more days, *i.e.* until the end of the spore-discharge period, which terminates only with the complete exhaustion of the hymenium. The stage of development of the hymenium is exactly the same as that for the hymenium represented in surface view in Fig. 146 (p. 416).

In Fig. 147, a dark area of the hymenium is passed through proceeding to the right from element no. 8 to element no. 34, a light area from element no. 34 to element no. 59, an intermediate area from

element no. 59 to element no. 63, and another intermediate area from element no. 1 to element no. 8. As indicated by the shading, the spores in the light area are unpigmented, in the intermediate areas partially pigmented, and in the dark area fully pigmented.

The hymenial elements can all be classified as basidia or paraphyses as follows: past-generations basidia, nos. 13, 21, 30, 38, and 51; present-generation basidia, nos. 3, 5, 11, 16, 24, 32, 41, 44, 48, 53, 57, and 61; coming-generation basidia, nos. 8, 18, 28, 36, 42, 46, 55, and 60; future-generations basidia, nos. 2, 6, 7, 9, 12, 14, 17, 19, 23, 27, 29, 31, 34, 37, 45, 49, 52, 54, 59, and 62; paraphyses (permanently sterile elements), nos. 1, 4, 10, 15, 20, 22, 25, 26, 33, 35, 39, 40, 43, 47, 50, 56, 58, and 63.

The past-generations basidia have shed their spores and are all dead. They were once as protuberant as the present-generation basidia but their ends are now drawn down to the general level of the hymenium. The free end of each past-generation basidium appears flattened in side view, but is in reality concave, the concavity concealing the sterigmatic stumps. The collapsed shafts are often somewhat brownish, a discoloration which aids one in the not too easy task of identifying them.

A basidium which fails for any reason to discharge its spores at the proper time, on collapsing, draws down its spores to the general level of the hymenium, so that they cannot interfere mechanically with the new spores developing on the sterigmata of neighbouring basidia. Two such undischarged or wasted spores which are now lying on, and adhering to, the hymenium, are shown in Fig. 147 at *w w*. Each of them was dragged down to its place of rest during the collapse of a past-generation basidium. The waste spore, *w*, on the right of the illustration, is supposed to have been produced by the element no. 51, but the basidium which produced the other waste spore is not shown.

The present-generation basidia all bear sterigmata and spores. Their bodies protrude above the general level of the hymenium to a distance of about 0·005 mm. The spores are raised up on sterigmata, where, during their development and discharge, they cannot be interfered with mechanically either by the wasted spores or by the tops of neighbouring younger basidia. The age of the spores

varies from about five minutes in no. 41 to about eight hours in nos. 24 and 32. Spores which are of full size but colourless are from forty minutes to two hours and forty minutes old (nos. 53 and 57). Spores which are undergoing pigmentation are from two hours forty minutes to four hours and forty minutes old (nos. 61, 3, and 5). Spores which are fully pigmented are from four hours and forty minutes to eight hours old (nos. 11, 16, 24, 32). These ages are approximations based on studies already recorded. The contents of the basidia are not shown but, if they were, we should see that the bodies of nos. 41, 44, and 48 were practically full of protoplasm and that the bodies of nos. 24 and 32 were empty. We should observe stages in the progressive emptying of the basidium-contents into the spores in nos. 53, 57, 61, 3, 5, 11, 16, and 24 : we should note the origin and increase in size of a basal vacuole in the basidium-body, and its extension upwards until it filled not only the whole basidium-body but also the sterigmata except perhaps their tips. Most of the basidia are bisporous, but two of them, nos. 48 and 57, are monosporous. The solitary sterigma of each of these is situated in line with the axis of the basidium-body. The spores of the monosporous basidia develop unilaterally on the ends of their sterigmata, and each possesses the usual hilum ; but they differ from the spores of the bisporous basidia in size. If one compares the spore on no. 57 with the spores on nos. 11, 53, or 61, one perceives that the former is distinctly longer, somewhat broader, and of about twice the volume of the latter.

Nos. 3 and 5 show the typical arrangement of the spores on any two very closely adjacent basidia which develop their spores simultaneously : the four spores are situated at the corners of a square or rectangle (*cf.* Fig. 146, lower right-hand corner at *b*, p. 416). This prevents any jostling of the spores during their development and discharge. The positions of the spores are decided by the positions of the sterigmata at their first origin ; and, as we have seen, the positions of the sterigmata appear to be decided by the positions which the centrosomes of the daughter nuclei in the basidium-body take up after their formation.[1] It seems probable, therefore, that the position of the spores in such

[1] *Cf.* p. 420.

Fig. 147.—*Psalliota campestris* (cultivated form). Cross-section of part of a living gill showing semi-diagrammatically the structure of the hymenium *h*, the subhymenium *s*, and part of the trama *t*. The gill is supposed to have been taken from a mushroom which has been shedding spores for about 24 hours and the hymenium of which will therefore not be totally exhausted for several days. A dark area of the hymenial surface is passed through proceeding to the right from element no. 8 to element no. 34, a light area from element no. 34 to element no. 59, an intermediate area from element no. 59 to element no. 63, and another intermediate area from element no. 1 to element no. 8. As shown by the shading, in the light area the spores are unpigmented, in the intermediate areas partially pigmented, and in the dark area fully pigmented.

The elements of the hymenium can be analysed as follows: past-generations basidia, nos. 13, 21, 30, 38, and 51; present-generation basidia, nos. 3, 5, 11, 16, 24, 32, 41, 44, 48, 53, 57, and 61; coming-generation basidia, nos. 8, 18, 28, 36, 42, 46, 55, and 60; future-generations basidia, nos. 2, 6, 7, 9, 12, 14, 17, 19, 23, 27, 29, 31, 34, 37, 45, 49, 52, 54, 59, and 62; paraphyses (permanently sterile elements which enlarge as the hymenium becomes more and more exhausted), nos. 1, 4, 10, 15, 20, 22, 25, 26, 33, 35, 39, 40, 43, 47, 50, 56, 58, and 63.

Parts of three waves of development are shown proceeding across the section from right to left. The rear end (about three-ninths) of the foremost wave consists of the series of basidia, nos. 51, 38, 32, 24, 16, 11, 5, and 3. The middle part (about four-ninths) of the next succeeding wave consists of the series of basidia nos. 61, 57, 53, 48, 44, 41, 36, 28, 18, and 8. The forepart (about two-ninths) of the third wave which succeeds the second, consists of the series of basidia nos. 60, 55, 46, 42, and 34. There is a difference of about eight and one-half hours between each basidium of one wave and its nearest neighbour of the preceding wave. Thus after eight and one-half hours the basidium no. 8 will approximately resemble no. 5 as it is now, no. 18 will resemble no. 16, no. 28 will resemble no. 24, etc.

The basidia of the rear part of the first wave will now be described. No. 51 has been in the collapsed condition for an hour or more; its concave end, drawn down to the general level of the hymenium, conceals the sterigmatic stumps. No. 38 is in the act of sudden collapse about twenty minutes after the discharge of its last spore; its end is rapidly becoming concave, and its sterigmata are being drawn into the concavity. No. 32 bears a spore which has a drop about ten seconds old and of the maximum size on its hilum and which therefore should be shot away at once. The other spore was shot away from its sterigma about a minute ago, in the direction indicated by the arrow, to a distance of about 0·1 mm. This spore is shown in its flight with the water-drop attached to it. No. 24 is about to shoot away its spores, for a water-drop is being rapidly excreted at each spore-hilum. The right-hand drop is about eight seconds old and of nearly maximum size which indicates that the spore to which it is attached should be shot away after the lapse of about two more seconds. The other drop is only about two seconds old and therefore will continue to grow for about eight more seconds. The spores on both no. 32 and no. 24 are about eight hours old. No. 16 bears fully pigmented spores which we may suppose to be six and one-half hours old and therefore an hour and a half from the moment of spore-discharge. No. 11 also has fully pigmented spores. These we may suppose to be five and a half hours old and therefore two and a half hours from the moment of spore-discharge. Nos. 5 and 3 may be supposed to have begun their development at the same moment. Their spores are becoming strongly pigmented, and we may conclude that they are about four hours old and four hours from discharge.

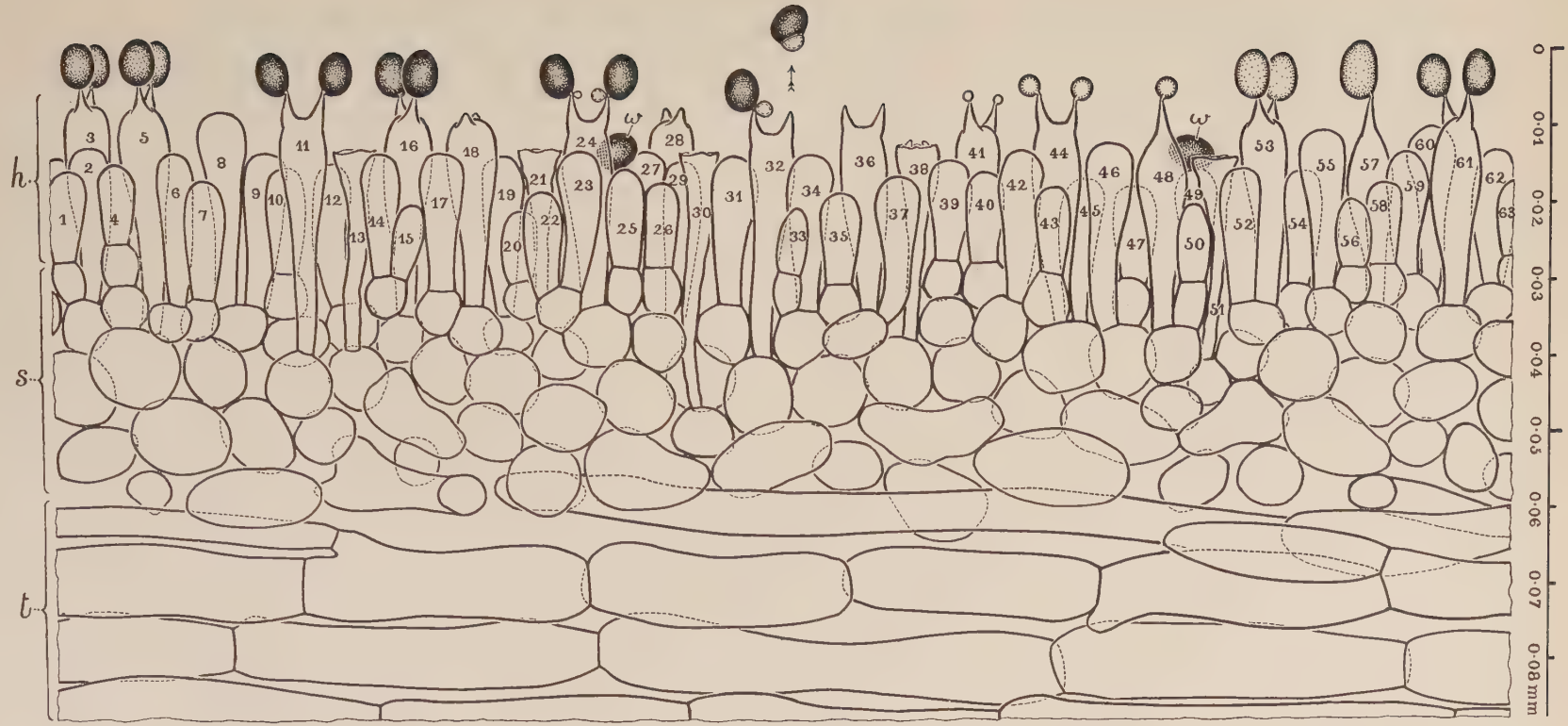
The basidia of the middle part of the second wave will now be described. No. 61 bears spores which are becoming pigmented. We may suppose them to be three and a half hours old. No. 57 bears a single sterigma and a spore of full size but unpigmented. We may suppose the spore to be two hours old. No. 53 bears two spores of full size but unpigmented. We may suppose them to be one hour old, so that they attained full size only twenty minutes ago. Nos. 48 and 44 bear spores which are far below full size and about ten minutes old. The spores of no. 41 are only five minutes old. No. 36 bears full-grown sterigmata but no spores as yet. It resembles in outward form a basidium which has just shot away its second spore, *i.e.* such a basidium as no. 32 will be like within two seconds when the left-hand spore has been discharged, but differs from it in being stuffed with contents instead of having its interior occupied by a large vacuole. No. 28 bears sterigmata about two-thirds developed and no. 18 sterigmata about one-third developed. No. 8 shows as yet not a trace of sterigmata.

The basidia of the forepart of the third wave will now be described. No. 60 is almost, if not quite, of full length. No. 55 has certainly not yet attained its full length, for it is not yet fully protuberant. Nos. 46 and 42 are progressively younger and less protuberant. No. 34, which forms the foremost element of the wave, is simply a future-generation basidium which does not yet protrude beyond the general level of the hymenium.

Most of the present-generation basidia are bisporous, but nos. 48 and 57 are monosporous. The spore on no. 57 has about twice the volume of any spore on a bisporous basidium. Nos. 3 and 5 show the typical arrangement of the spores on any two very closely adjacent basidia which happen to develop their spores simultaneously: the four spores are situated at the four corners of a square or rectangle. Two waste spores, *w w*, are shown lying on the hymenium; the basidia to which they belonged failed to discharge them and they were therefore dragged down on to the hymenium when these basidia collapsed. We may suppose that the basidium no. 51 shot away one of its spores successfully but not the other; hence the waste spore adjacent to its free end.

The subhymenium *s* consists of several layers of rounded or oval cells. There is no sharply defined level plane separating the hymenium from the subhymenium. The older basidia (the first to develop spores) arise very deeply in the subhymenium, *e.g.* nos. 30 and 51; but nos. 5, 11, 13, and 38 are also noteworthy in this respect. The basidia which successively come to maturity during the several days of spore-discharge arise more and more toward the top of the hymenium and have shorter and shorter bodies. The trama *t* consists of elongated cells forming irregularly anastomosing chains which tend to run in a direction parallel to the median line of the cross-section of the gill.

Magnification, 1,060. The scale is divided into hundredths of a mm.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a pair of basidia as 3 and 5 is decided by stimuli which affect the nuclei. Exactly how these stimuli operate is at present a matter for speculation. It may be that mutual stimuli are conducted from one basidium to the other by means of protoplasmic connections passing through one or more cells of the subhymenium; or, possibly, stimuli are provided by the mutual pressure of the basidia, by a gaseous emanation, or by transpiration. Possibly some day the matter may be decided by performing minute operations on the hymenium with the aid of instruments for microdissection such as have been used by Kyte. The mutual adjustment of the positions of the spores on neighbouring basidia only takes place when the basidia producing the spores simultaneously are in contact or nearly in contact; but basidia which are relatively distant from one another, *e.g.* nos. 11 and 16, do not seem to influence one another in any way, and a prediction of the probable relative positions of their spores is impossible. The corners-of-a-square arrangement of the spores of two adjoining bisporous basidia of a Cultivated Mushroom exactly resembles the corners-of-a-square arrangement of the four spores of a quadrisporous basidium of the Wild Mushroom. Two adjoining bisporous basidia, therefore, appear to respond to the stimulus which decides the positions of the spores like the two halves of a quadrisporous basidium.

The coming-generation basidia (nos. 8, 18, 28, 36, 42, 46, 55, and 60) are destined to produce the next crop of spores after the spores on the sterigmata of the present-generation basidia have been discharged. Like the present-generation basidia they are distinctly protuberant, but they differ from these in that they do not bear spores. They develop sterigmata in the later stages of their growth. Nos. 42, 46, and 55 are not yet fully protuberant, as they are relatively young: they are associated with present-generation basidia which bear very rudimentary spores. On the other hand, nos. 60, 8, 18, 28, and 36 are fully protuberant, for their bodies have attained maximum length: they are associated with present-generation basidia which bear relatively mature spores. The cell-contents are not shown but, if they were, we should see that the body of each coming-generation basidium was filled, or almost completely filled, with fine protoplasm.

The future-generations basidia (nos. 2, 6, 7, 9, 12, 14, 17, 19, 23, 27, 29, 31, 34, 37, 45, 49, 52, 54, 59, and 62) are smaller than those of the coming-generation basidia and never bear sterigmata. They are not yet protuberant; indeed, it is their free ends, together with those of the past-generation basidia and of many of the paraphyses, which make up what I have often referred to as the *general level of the hymenium*, above which the bodies of the basidia of the present-generation and coming-generation basidia project by about 0·005 mm. The basidium-bodies are filled with fine protoplasmic contents. Since the hymenium represented in Fig. 147 is supposed to have been discharging spores for only 24 hours and will discharge further spores for some four or five days, the future-generations basidia still outnumber those of the past generations.

The paraphyses (nos. 1, 4, 10, 15, 20, 22, 25, 26, 33, 35, 39, 40, 43, 47, 50, 56, 58, and 63) are permanently sterile: they never produce sterigmata or spores. They are usually attached to the uppermost cells of the subhymenium and are the shortest of the hymenial elements. At the stage of the development of the hymenium shown in Fig. 147 (p. 429), they have not yet grown to their maximum size. As more and more generations of basidia shed their spores and collapse, the paraphyses grow larger and larger in diameter, so that the lateral space which they occupy in the hymenium is progressively increased. Drawings of older swollen paraphyses will be given in a subsequent illustration. The paraphyses in the hymenium represented in Fig. 147 are to a large extent covered laterally by the bodies of the basidia. Owing to their small size in the young hymenium and to the fact that they are largely hidden by the basidia, they are often difficult to make out clearly. At first they contain a large amount of protoplasm in which one can usually detect one or more vacuoles; but, as they grow older and enlarge, their vacuoles increase in size and their massive protoplasm gradually disappears, so that, finally, in late stages of the development of the hymenium, the lumen of each paraphysis comes to be occupied by one large vacuole.

Parts of three waves of development are shown in Fig. 147 (p. 429) proceeding across the section from right to left. The rear end (about three-ninths) of the earliest wave consists of the series of

basidia nos. 51, 38, 32, 24, 16, 11, 5, and 3. The middle part (about four-ninths) of the next succeeding wave consists of the series of basidia nos. 61, 57, 53, 48, 44, 41, 36, 28, 18, and 8. The fore part (about two-ninths) of the third wave, which succeeds the second, consists of the series of basidia nos. 60, 55, 46, 42, 34, and 31. The stretch of hymenium shown in the illustration is unfortunately too short to show the whole length of any one wave: but a whole wave can easily be imagined if we suppose that the illustration is enlarged by adding to its left side in succession two copies of it. With this arrangement we should have the following set of basidia making a complete wave: nos. 51 (the hindmost element), 38 (the wave declining), 32 (crest of the wave: spore-discharge), 24 (beginning of the fore part of the wave), 16, 11, 5, 3, 61, 57, 53, 48, 44, 41, 36, 28, 18, 8, 60, 55, 46, 42, 34, and 31 (the foremost element of the wave). There is a difference in development of about eight and one-half hours between each basidium of the second of the three waves and its nearest neighbour of the first wave. Thus, for instance, after about eight and one-half hours, the basidium no. 28 will resemble no. 24 as it is now, no. 18 will resemble no. 16, and no. 8 will resemble no. 5. There is a similar difference between the third wave and the second. Thus, after about eight and one-half hours, the basidium no. 55 will resemble either no. 53 or no. 57, and no. 46 will resemble either no. 44 or 48.

The basidia of the rear part of the first wave will now be described. No. 51 has been in the collapsed condition for an hour or more; its concave end, drawn down to the general level of the hymenium, conceals the sterigmatic stumps. No. 38 is in the act of sudden collapse about 20 minutes after the discharge of its last spore; its end is rapidly becoming concave and the sterigmata are being drawn into the concavity. No. 32 bears a spore which has a drop about 10 seconds old and of the maximum size on its hilum and which, therefore, should be shot away at once. The other spore was shot away from its sterigma about a minute ago, in the direction indicated by the arrow, to a distance of about 0·1 mm. This spore is shown in its flight with the water-drop attached to it. No. 24 is about to shoot away its spores, for a water-drop is being rapidly excreted at each spore-hilum. The

right-hand drop is about eight seconds old and of nearly maximum size, which indicates that the spore to which it is attached should be shot away after the lapse of about two more seconds. The other drop is only about two seconds old and therefore will continue to grow for about eight more seconds. The spores on both no. 32 and no. 24 are about eight hours old. No. 16 bears fully pigmented spores, which we may suppose to be six and one-half hours old and therefore an hour and a half from the moment of spore-discharge. No. 11 also has fully pigmented spores. These we may suppose to be five and a half hours old and therefore two and a half hours from the moment of spore-discharge. Nos. 5 and 3 may be supposed to have begun their development at the same moment. Their spores are becoming strongly pigmented, and we may therefore suppose that they are about four hours old and four hours from the moment of spore-discharge.

The basidia of the middle part of the second wave will now be described. No. 61 bears spores which are becoming pigmented. We may suppose them to be three and a half hours old. No. 57 bears a single sterigma and a spore of full size but unpigmented. We may suppose the spore to be two hours old. No. 53 bears two spores of full size but unpigmented. We may suppose them to be one hour old, so that they attained full size only twenty minutes ago. Nos. 48 and 44 bear spores which are far below full size and about ten minutes old. The spores on no. 41 are only five minutes old. No. 36 bears full-grown sterigmata but no spores as yet. It resembles in outward form a basidium which has just shot away its second spore, *i.e.* such a basidium as no. 32 will be within two seconds when the left-hand spore has been discharged. But one can easily distinguish between a basidium which is just about to develop its spores and one which has just discharged them, for there is a marked difference in their cell-contents. The former has a basidium-body filled or almost filled with protoplasm, while the latter has a basidium-body occupied by one large vacuole. No. 28 bears sterigmata about two-thirds developed, and no. 18 sterigmata about one-third developed. Finally, no. 8 shows as yet not even a trace of sterigmata.

We shall complete the account of the basidia entering into the

three hymenial waves by describing the basidia of the fore part of the third wave. No. 60 is almost, if not quite, of full length. No. 55 has certainly not attained its full length and is therefore not yet fully protuberant. Nos. 46, 42, and 34 are progressively younger and less protuberant. No. 31 which forms the foremost element in the wave is simply a future-generation basidium, which does not yet protrude beyond the general level of the hymenium.

The subhymenium *s* consists of some three or four layers of rounded or oval cells. There is no sharp and level plane separating the hymenium from the subhymenium, such as many writers have imagined. Some of the basidia, namely, the oldest (the earliest to develop spores), arise very deeply in the subhymenium, either toward its middle or sometimes even lower. In Fig. 147 (p. 429), the most striking basidia, so far as depth of origin is concerned, are nos. 30 and 51, but nos. 5, 11, 13, and 38 are also noteworthy in this respect. The basidia which successively come to maturity during the several days of the spore-discharge period arise more and more toward the top of the subhymenium. The paraphyses are situated quite superficially: the small subhymenial cells from which so many of them arise appear to be almost pedicellar in their nature (*cf.* the cells beneath the paraphyses nos. 1, 4, 10, 25, 26, 33, etc.).

The trama *t* consists of large elongated cells attached together in chains which are irregularly anastomosing and which tend to run in a direction parallel to the median line of a cross-section of the gill. Sometimes there are a few narrow elongated hyphae just beneath the subhymenium where the trama begins. Some have been represented in Fig. 147.

At the stage of development shown in Fig. 147 (p. 429), the hymenium contains a great deal of protoplasm and accumulated food-stuffs. Cell-contents are particularly heavy in the younger present-generation basidia, in the coming-generation and in the future-generations basidia. There is a less amount of protoplasm in the paraphyses. On account of the presence of heavy cell-contents, the hymenium appears very dense even in thin sections, which fact constitutes one of the difficulties in making out the cell-outlines. The subhymenium also contains a large quantity of

protoplasm, and a less amount is present in the cells of the trama. Part of this protoplasm and its inclusions, such as glycogen, etc., is doubtless used up in the growth of the basidia in length and of the paraphyses in breadth, and part of it is necessary for the formation of the sterigmata and the spore-walls. Part of it must also be used up in processes of destructive metabolism, including respiration. But there can be little doubt that most of it is destined to pass through the narrow sterigmatic necks and to be crowded into the spores, there to await the important process of germination and the construction of germ-tubes. As more and more generations of basidia shed their spores, the hymenium, subhymenium, and trama become more and more emptied of protoplasm, until, when the process of spore-discharge ceases, the cells are all occupied by large vacuoles. The contrast in density between a section of a gill which has just begun to shed spores, and of a gill which has just ceased to shed spores, is very striking. No doubt, chemical analysis of two such sections would show a very marked difference in proteins and other cell-contents. There is every reason to suppose that a mushroom must be much more nutritious when it is young than when it is aged, for the most desirable food substances which it contains are gradually carried away from the pileus by the spores during the spore-discharge period.

The Hymenium of the Wild Mushroom.—Up to the present we have confined our analysis of the hymenium to the cultivated form of *Psalliota campestris*. We shall now turn to the wild form, the hymenium of which is similar in all essentials of its organisation to that of the cultivated form, although it exhibits some interesting differences in detail. The main points of difference are: (1) the Wild Mushroom, typically, has quadrisporous basidia and the Cultivated Mushroom bisporous ones, (2) the basidia of the Wild Mushroom are distinctly larger than those of the Cultivated, and they produce longer spores (*cf.* Figs. 148 and 149 with Fig. 147, p. 429).

The cross-section of the Cultivated Mushroom represented in Fig. 147 (p. 429), which has just been described, is a synthetic one, embodying as many morphological details as possible; but it is unaccompanied with drawings of any of the special sections

upon which it was based. In the case of the Wild Mushroom, on the other hand, no synthetic drawings will be given, and we shall confine our attention to a set of special sections from which a synthetic illustration might be constructed, were such required. Our plan will be to study a series of such sections which show the hymenium in: (1) an early stage of its activity, (2) an almost exhausted stage, and (3) a completely exhausted stage. These sections were all cut with a hand-razor from living gills and mounted in water, after which the cells were drawn with the *camera lucida*. The illustrations representing these sections on subsequent pages of this Chapter are the first of their kind to be published, and I shall not hesitate, therefore, to tell the secret of my success in making them. I used perfectly fresh mushrooms, cut sections through the thickest part of a gill with a sharp razor held in the hand, examined the sections in the living state immediately after they had been mounted in water, and interpreted the sections in the light of the knowledge and experience which I had gained during my study of *Panaeolus campanulatus* and *Stropharia semiglobata*. The microscope employed was a Zeiss, eyepiece no. 4 and objective FF. The original *camera-lucida* sketches were made with a magnification of 1,040 diameters and then photographed with a lantern-slide-making apparatus. The negatives so obtained were then put into a lantern and projected on a sheet of white paper, so that the magnification of the original drawings was increased from 1,040 diameters to 1,560. The projections were then traced out on the paper with a pencil. The tracings so obtained were then made into black-and-white drawings with ink, and these drawings, after reduction to two-thirds by the block-maker, are reproduced as Figs. 148–152.

The illustrations of the special sections, about to be described, not only show the general succession of basidia but exhibit for the first time, so far as the Mushroom is concerned: (1) collapsed past-generations basidia which hitherto have been overlooked, (2) paraphyses which never produce spores and are destined from the first to remain sterile, and (3) the true relations of the hymenial elements with the subhymenium.

Camera-lucida Studies of the Young Hymenium.—In Fig. 148

is represented part of a cross-section of a living gill of a fruit-body which had just expanded and had only very lately commenced to shed spores. The past-generation basidia were so few in number that none happened to be included in the section. In cutting the section, some of the spores on the basidia nos. 1, 2, and 3 were either displaced or knocked off their sterigmata, while the riper spores on nos. 4 and 5 were all knocked off. The details of the spores and sterigmata of these five basidia have been adjusted semi-diagrammatically ; but all the other cells are shown as observed. It may be remarked that nearly ripe spores are very easily detached from their sterigmata by the pressure of surface tension when the section to which they belong is irrigated with water ; and the premature detachment of the riper spores is probably a mutilation characteristic of all preparations mounted in fluids. Histologists should beware of being deceived by the supposition that a hymenium, after being fixed and stained and cut into sections with the microtome, necessarily exhibits all the delicate morphological relations which the living hymenium possesses in nature. The section shown in Fig. 148, although not including any past-generation basidia, includes five present-generation basidia, nos. 1, 2, 3, 4, and 5. These, as indicated by the degrees of pigmentation of the spores, form part of a wave of development progressing from the right-hand to the left-hand side of the section. Two coming-generation basidia, nos. 6 and 7, have both attained about their maximum protuberancy and, doubtless, are preparing for the production of sterigmata. The future-generations basidia are nos. 8, 9, 10, 11, 12, 13, 14, 15, 16, and 17. Their free ends, which are not yet protuberant, constitute the general level of the hymenium. The permanently sterile elements or paraphyses are nos. 18, 19, 20, 21, and probably no. 22. But how, it may be asked, does one really know that these elements are paraphyses ? Why should they not be very young basidia which subsequently will produce spores ? These questions are certainly pertinent and demand an answer. Now a study of the progressive exhaustion of the hymenium and of the completely exhausted hymenium proves (*vide infra*) that a large number of elements in the hymenium never produce spores but gradually enlarge in diameter, as the hymenium gets

older, without growing appreciably in length. In the exhausted hymenium these cells are found to be short elements which have a superficial origin from the subhymenium. But, in the section we

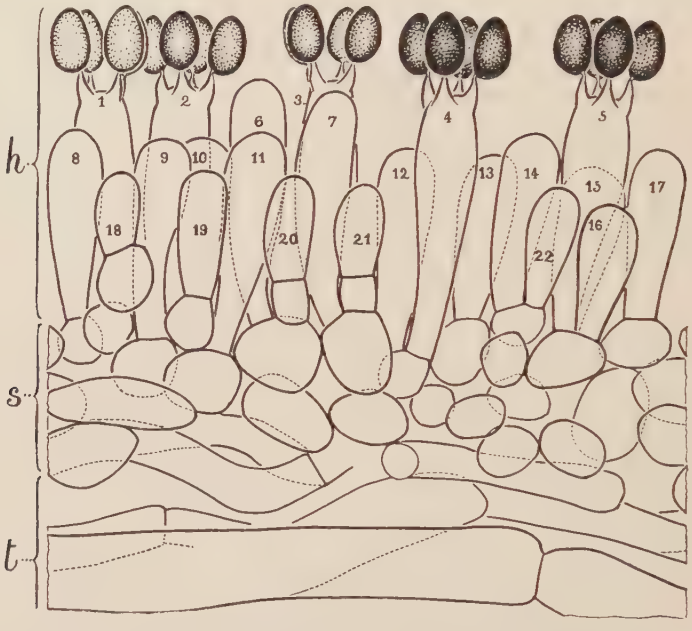

FIG. 148.—*Psalliota campestris* (wild form). Cross-section of a living gill of a fruit-body just expanded, drawn with a *camera lucida*. In cutting the section some of the spores on the basidia nos. 1, 2, and 3, were either displaced or knocked off their sterigmata, while the riper spores on nos. 4 and 5 were all knocked off. The details of the spores and sterigmata of these five basidia have been adjusted semi-diagrammatically. All the other cells are shown as observed. Special objects of drawing: to show (1) presence of paraphyses and (2) relations of hymenium with subhymenium. *h*, the hymenium; *s*, the subhymenium; and *t*, part of the trama. Nos. 1, 2, 3, 4, and 5, present-generation basidia. Nos. 6 and 7, coming-generation basidia. Nos. 18, 19, 20, 21, and probably 22, are paraphyses. The elements nos. 4, 7, 21, etc., arise at diverse levels of the subhymenium. Magnification, 1,040.

are discussing, the elements nos. 18, 19, 20, 21, and 22 are the shortest elements; of all the elements present they resemble basidia least; moreover, they are seated on the outermost subhymenial cells. Their contents are already provided with large vacuoles (although this is not indicated in the illustration), as if they were already beginning to empty themselves, and were thus

coming to resemble the paraphyses with clear lumina which certainly occur in a fully exhausted hymenium. All the other cells in the section are too long to be paraphyses, as will be seen by comparing Figs. 148 and 152, A (p. 448). The process of elimination, by itself, therefore, leads to the conclusion that the elements nos. 18, 19, 20, 21, and 22 are paraphyses. This conclusion is also supported by comparative studies of other hymenia such as those of *Panaeolus campanulatus* and *Stropharia semiglobata*, where the elements are much larger and more easily differentiated from one another.

A study of Fig. 148 shows that there is no sharp and level plane dividing the hymenium from the subhymenium, for the bases of the hymenial elements are situated at very various levels in the subhymenium. In this regard the basidium no. 4 is noteworthy, for it arises at about the middle depth of the subhymenium. On the other hand, basidia nos. 13 and 7 arise at a higher level, and the paraphyses nos. 20 and 21 at a still higher level. The large subhymenial cell which has given rise to the basidium no. 6 has also produced a small subhymenial cell which acts as a pedicel for the paraphysis no. 20. A similar relation appertains for the basidium no. 7 and the paraphysis no. 21. The same subhymenial cell no doubt often produces at least two and possibly more basidia, but no good instance of this is shown in this particular illustration.

The section shown in Fig. 149 was cut from the same mushroom and at the same time as the one which has just been described. The spores on basidium no. 1 were bent out of their normal positions in cutting the section and have been readjusted semi-diagrammatically. The other cells are all drawn as observed. Here again, there are no past-generations basidia to be seen : one might have been included in the section but was not. Nos. 1, 2, and 3 are present-generation basidia, evidently bearing very young spores, for the spores on nos. 2 and 3 are only partly grown, while those on no. 1, although of full size, are as yet unpigmented. Nos. 4, 5, and 6 are coming-generation basidia, a fact indicated by their protuberancy which is greatest in no. 6. Basidia nos. 1, 2, 3, and 6 appear to form part of a wave of development which is passing across the section from left to right. Nos. 7, 8, 9, 10, 11, and 12

are future-generations basidia, while nos. 13, 14, 15, 16, and 17 from their size, position, and contents appear to be paraphyses.

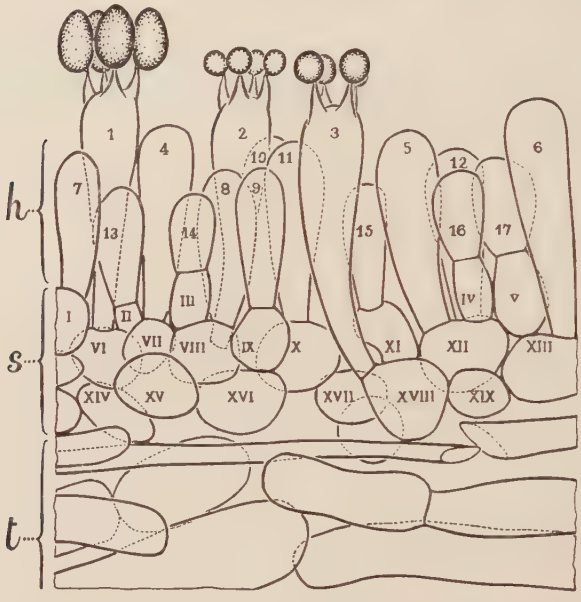

FIG. 149.—*Psalliota campestris* (wild form). Cross-section of a living gill of a just expanded fruit-body, drawn with the *camera lucida*. The spores on basidium No. 1 were bent out of their normal positions and have been adjusted semi-diagrammatically. To show (1) paraphyses, and (2) relations of hymenium and subhymenium. *h*, the hymenium; *s*, the subhymenium; *t*, part of the trama. Nos. 1, 2, and 3, present-generation basidia. Nos. 4, 5, and 6, coming-generation basidia. Nos. 7, 8, 9, 10, 11, and 12, basidia of future generations. Nos. 13, 14, 15, 16, and 17, paraphyses. From the uppermost layer of the subhymenium, cells I, II, III, IV, and V, arise paraphyses or occasionally, as from cell I, a basidium; from the second layer, cells VI, VII, VIII, IX, X, XI, XII, and XIII, arise either basidia or cells supporting paraphyses, or occasionally, as from cell XI, a paraphysis; from the lowest layer, cells XIV, XV, XVI, XVII, XVIII, and XIX, arise sometimes a basidium as at XVIII or, more frequently, cells of the second layer of the subhymenium. Magnification, 1,040.

The subhymenium can be divided roughly into three layers. The highest layer, cells nos. I, II, III, IV, and V, chiefly give rise to paraphyses; from the second layer, cells VI, VII, VIII, IX, X, XI, XII, and XIII, arise occasionally a paraphysis as from no. XI,

but more usually either basidia or cells supporting paraphyses; from the lowest layer, cells nos. XIV, XV, XVI, XVII, XVIII, and XIX, arise sometimes a basidium as at XVIII, but more frequently cells of the second layer of the subhymenium. Here again, it is clear that there is no level plane separating the hymenium from the subhymenium. The basidium no. 3 arises from one of the lowest cells of the subhymenium, whereas the basidia nos. 11 and 5, etc., arise at a higher level, and the paraphyses nos. 14 and 16, etc., at a still higher level. The oldest basidia, *i.e.* those which produce spores first, are as a rule the longest, owing to their depth of origin in the subhymenium. Basidia of later generations tend to arise more and more superficially, so that their shafts become shorter and shorter. In this particular section, the basidia nos. 1, 2, and 3, which alone are producing spores, are the most deep-seated so far as their origin is concerned.

Between the subhymenium and the swollen cylindrical cells of the trama, there are often placed a certain number of thin elongated hyphae. One of these happens to be present in Fig. 149.

The last of the sections of the very young hymenium, cut at the same time as the two just described, is represented in Fig. 150. In cutting and mounting the section, all the spores on basidia nos. 1, 2, 3, 4, and 5 were knocked off their sterigmata except the one shown on no. 1. Probably the spores on all these basidia were nearly ripe and, on this account, easily detachable. None of the spores accidentally removed are restored in this Figure, so that the present-generation basidia are all represented in their mutilated condition. It may be asked: is it not possible that the basidia nos. 2, 3, 4, and 5 are really basidia which have just shot away their spores? The answer is no. These basidia all contained a certain amount of massive protoplasm in their upper ends (not shown in the illustration) which was doubtless still being passed into the spores; but such protoplasm is not contained in basidia which have just shot away their spores. Moreover, basidia which have shot away their spores usually collapse about twenty minutes after the discharge of the last spore. It is most unlikely that four basidia, which have discharged all their spores and are all about

to collapse together, should be contained in one small section such as is here represented. There is only one coming-generation basidium, namely, no. 6. Others, doubtless, were only just missed when the section was cut. The future-generations basidia are nos. 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, and 18. The paraphyses are nos. 19, 20, 21, and 22, and possibly nos. 7 and 9 ; but I have assumed that nos. 7 and 9 are very short basidia on account of their being already so broad in an early stage of the development of the hymenium. The contents of nos. 7 and 9, unfortunately, were not observed. It is likely that there were paraphyses attached to the subhymenial cells nos. V and VI, but that they were torn away in cutting the section. Other paraphyses, resembling no. 19 with its subhymenial cell no. III and no. 21 with its subhymenial cell no. IV, may have been just excluded from the section. One such set of cells would fit in nicely in front of basidium no. 13, from which position it may well have been removed. Once more we can notice the absence of any level plane separating hymenium and subhymenium. The oldest basidia, or at least some of the oldest, are the longest of all. Nos. 2 and 4 are remarkable for the depth to which their shafts descend to attach themselves to subhymenial cells of the lowest layer. The basidium no. 2 arises from the cell no. XXIII, and no. 4 from no. XXIX ; and the lower part of the basidial shaft of each is completely enveloped by subhymenial cells. With the position of origin of basidium no. 2 should be compared the positions of origin for elements nos. 10, 9, and 19 ; and with the position of origin of basidium no. 4 should be compared the positions of origin for elements nos. 15, 16, and 21. The subhymenium consists of rounded or oval cells, and can be divided very roughly into four rows of cells : I to VI inclusive, VII to XXI inclusive, XXII to XXXIII inclusive, and a fourth layer of a few cells only, XXXIV to XXXVI inclusive. The paraphyses are always superficial in their origin, but basidia arise at various levels of the hymenium, the older ones tending to be most deeply seated and the younger ones to be situated more and more toward the exterior.

A little more of the trama is shown in Fig. 150 than in the two preceding Figures. It will be noticed that the larger tramal cells,

which tend to form cell-chains, greatly exceed in size even the largest elements of the hymenium and subhymenium.

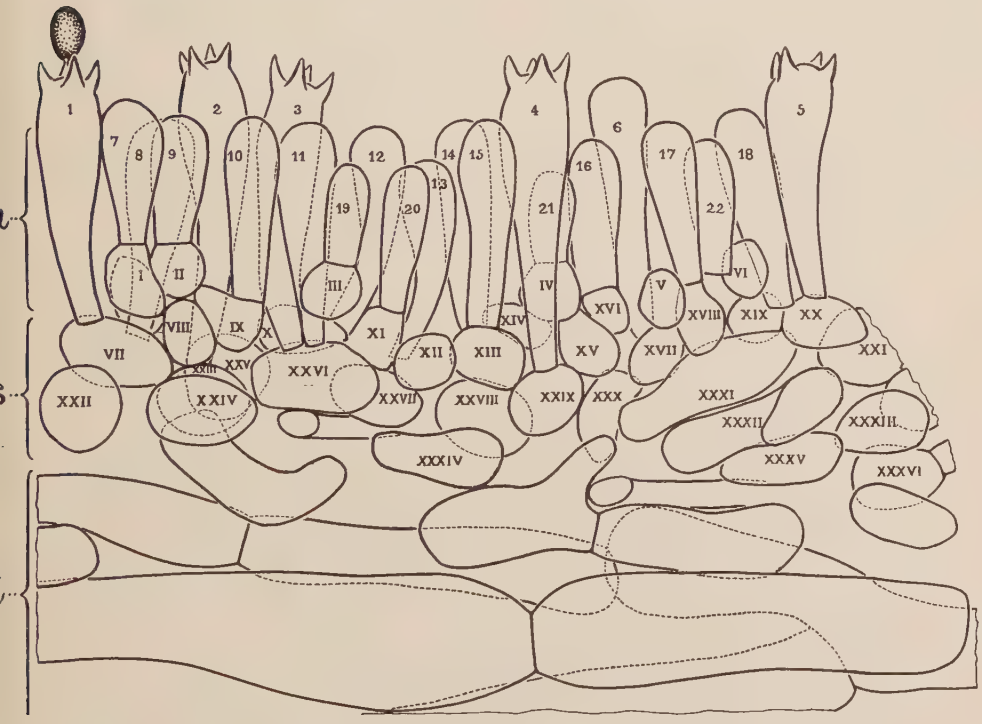

FIG. 150.—*Psalliota campestris* (wild form). Cross-section of a living gill of a fruit-body just expanded, drawn with the *camera lucida*. In cutting the section all the spores on the basidia nos. 1, 2, 3, 4, and 5, were knocked off their sterigmata except the one shown on basidium no. 1. The extreme top and bottom of basidium no. 6 were not drawn owing to an oversight, and have been completed semi-diagrammatically; otherwise all elements are represented as seen. Chief object of drawing: to show the relations of the hymenium with the subhymenium. *h*, the hymenium; *s*, the subhymenium; *t*, part of the trama. Nos. 1, 2, 3, 4, and 5, present-generation basidia. No. 6, a coming-generation basidium. Nos. 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, and 18, future-generations basidia, possibly with the exception of nos. 7 and 9 which may be paraphyses. Nos. 19, 20, 21, and 22, and possibly also nos. 7 and 9, are paraphyses. The subhymenium consists roughly of four layers of cells (reading from left to right): the highest layer, usually supporting paraphyses, I, II, III, IV, V, and VI; a second layer, VII, VIII, IX, X, XI, XII, XIII, XIV, XV, XVI, XVII, XVIII, XIX, XX, and XXI; a third layer, XXII, XXIII, XXIV, XXV, XXVI, XXVII, XXVIII, XXIX, XXX, XXXI, XXXII, and XXXIII; a fourth layer of a few cells only, XXXIV, XXXV, and XXXVI. Some of the basidia arise deep down in the subhymenium, *e.g.* nos. 2 and 4 which spring from the cells XXIII and XXIX respectively: the bases of these basidia are enveloped by upper subhymenial cells. It is evident from a study of this Figure that there is no sharp plane of demarcation between the hymenium and subhymenium. Magnification, 1,040.

Camera-lucida Studies of a Nearly Exhausted Hymenium.—The studies of the hymenium represented in Fig. 151 were made upon an old and nearly exhausted mushroom obtained from a field in England. The top of the mushroom was flat, and the gills were of a dark reddish-brown colour, indeed almost black; but the mottling of the hymenial surface could still be discerned. Evidently the fruit-body had been shedding spores for some days and was nearing the point of exhaustion. Sections of the living gills were made with a hand-razor as before, and two of them are shown at A and B in Fig. 151.

In Fig. 151, A, the elements nos. 1, 2, and 3 are present-generation basidia from all of which the spores were knocked off in cutting the section as at no. 3; but in nos. 1 and 2 the spores have been restored semi-diagrammatically. No. 4 is an old past-generation basidium arising deep down in the subhymenium from the cell no. VIII. The outlines of the other past-generations basidia cannot be clearly discerned, but it is evident that their gelatinised tops make up the general level of the hymenium which can be seen at *l*. There are no coming-generation basidia included in the section. Elements nos. 5, 6, and 7 are paraphyses. Two waste spores, *w*, are lying on the hymenium. The subhymenium consists roughly of three layers of cells: I to IV inclusive, V to VII inclusive, and VIII to X inclusive. It is evident that the past-generations basidia have all disappeared from the section except no. 4; otherwise it would be possible to observe their outlines and their attachments to the cells of the two upper layers of the subhymenium.

In Fig. 151, B, the elements nos. 1 and 2 are present-generation basidia from which the spores were knocked off in cutting the section; but for no. 2 the spores have been restored semi-diagrammatically. Nos. 3 and 4 are coming-generation basidia, the presence of which indicates that the mushroom, although old, would continue to discharge spores for at least half a day and possibly for twenty-four hours longer. The past-generations basidia which can be clearly distinguished are elements nos. 5, 6, 7, 8, and 9. The tops of other past-generations basidia, the walls of which have apparently been gelatinised, make up the

general level of the hymenium *l*. In the unclear spot, *u*, no

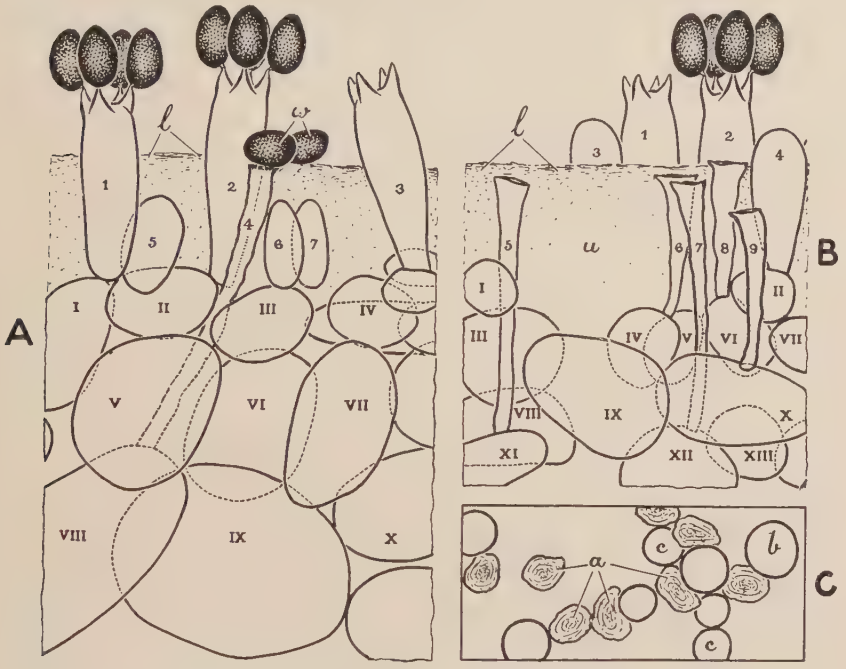

FIG. 151.—*Psalliota campestris* (wild form). *Camera-lucida* drawings of an old, nearly exhausted hymenium showing past-generations basidia arising at various levels of the subhymenium. A and B are cross-sections. In A, the elements nos. 1, 2, and 3 are present-generation basidia from which the spores were knocked off in cutting the section as at 3; but in 1 and 2 the spores have been restored semi-diagrammatically; no. 4, an old past-generation basidium arising from the subhymenial cell no. VIII; nos. 5, 6, and 7 are paraphyses; *l*, the general level of the hymenium including tops of no longer distinct past-generations basidia; *w*, waste spores lying on the hymenium; the subhymenium consists roughly of three layers of cells: I, II, III, and IV; V, VI, and VII; VIII, IX, and X. In B, nos. 1 and 2 are present-generation basidia from which the spores were knocked off, but for no. 2 the spores have been restored semi-diagrammatically; nos. 3 and 4, coming-generation basidia; nos. 5, 6, 7, 8, and 9, past-generations basidia; nos. 5 and 7, the longest and oldest, arise from near the base of the subhymenium; nos. 9, 6, and 8 arise successively at higher levels, while the basidium no. 4 arises at a still higher level; *u*, unclear spot where outlines of the cells could not be distinguished; *l*, general level of the hymenium made of indistinct tops of past-generations basidia; there are roughly four layers of subhymenial cells: I, II; III, IV, V, VI, VII; VIII, IX, X; XI, XII, XIII; basidia arise at all these levels. C, a surface view of the hymenium of the same material, showing such elements as could be clearly distinguished; *a*, past-generation basidia (as seen in water, brownish and with no distinguishable sterigmatic stumps); *b*, a coming-generation basidium; *c c*, small paraphyses. Magnification, 1,040.

individual element can be made out. The absence of any level plane sharply separating the hymenium from the subhymenium is

especially clear in this section. The subhymenium consists roughly of the following four layers of cells : I and II, III to VII inclusive, VIII to X inclusive, and XI to XIII inclusive. Now it will be noticed that the basidia are attached at very various depths to the cells of the subhymenium. The basidia nos. 5 and 7 are attached to the cells XI and XII, respectively, which belong to the deepest layer of the subhymenium. The basidia nos. 9, 6, 8, and 4 arise successively at higher and higher levels, and in consequence their shafts are shorter and shorter.

If one compares the basidia nos. 1, 2, and 3 in Fig. 151, A, and no. 4 in B, *i.e.* some of the last basidia to produce spores in an old hymenium, with basidia nos. 1, 2, and 3 in Fig. 149 (p. 440), nos. 1, 2, 3, 4, and 5 in Fig. 150 (p. 443), and nos. 4 and 5 in Fig. 148 (p. 438), *i.e.* with some of the earliest basidia to produce spores in a young hymenium, one can at once perceive that the former set of basidia is much shorter than the latter set. The comparison of hymenial sections from a mushroom at different ages seems to show that, in general, the first basidia to come to maturity, *i.e.* to produce spores, are the longest, the last basidia to produce spores are the shortest, and that there is a tendency to gradual shortening of the basidia coming to maturity as the hymenium becomes more and more exhausted.

In Fig. 151, C, is shown a surface view of the hymenium taken from the same material as the sections A and B. The hymenium was submerged in water under a cover-glass. Only such elements are shown as could be clearly distinguished. The past-generations basidia, *a*, were brownish. Their sterigmatic stumps could not be seen ; possibly they were disappearing or had disappeared. The large element *b* is a coming-generation basidium, and the elements *c* are paraphyses. As already explained in an earlier section, in the Mushroom, on account of the small size of the hymenial elements, the optical difficulties are too great to permit of one clearly distinguishing all the elements in a face view of the hymenium. The clear spaces left in the drawing C indicate that the cells in those regions seemed too vague and uncertain in their outlines to be worth sketching. The elements which have actually been drawn, with the exception of *b*, appear to be either

past-generations basidia or paraphyses. No present-generation basidium happened to be included in the area.

Camera-lucida Studies of a Completely Exhausted Hymenium.—The studies of the hymenium represented in Fig. 152 were made upon a completely exhausted mushroom which had discharged spores for six days and six nights. The sections were cut with a hand-razor a few hours after the last spores had been shed. In many of the cross-sections, one of which is represented at A, only the paraphyses could be made out, and the basidia, all of which belonged to past generations, were only represented by their gelatinised remains. In Fig. 152, A, the hymenium *h* is composed of paraphyses which still have clear outlines. All these cells were devoid of protoplasm and in this respect resembled the cells of the subhymenium *s* and trama *t*. The paraphyses, *p*, evidently correspond to the elements nos. 18, 19, 20, 21, and 22 in Fig. 148 (p. 438) and to nos. 13, 14, 15, 16, and 17 in Fig. 149 (p. 440). They were smaller when the hymenium began to discharge spores and have become somewhat swollen during the gradual exhaustion of the hymenium. The paraphyses, *g g*, appear to have arisen as outgrowths from the uppermost subhymenial cells, *i.e.* from cells like nos. I, II, III, IV, and V in Fig. 149 (p. 440) and like the cells upon which the paraphyses nos. 18, 19, 20, and 21 are situated in Fig. 148 (p. 438). The past-generations basidia have disappeared except for their gelatinised remains, which are indicated at *r r*. There are a number of waste spores, *w*, lying on, and adherent to, the hymenium.

In the drawing B of Fig. 152 is represented a piece of a section of the totally exhausted hymenium in which, in addition to the paraphyses *p*, two past-generations basidia can still be recognised at *b*. Their bodies were very faintly outlined and are so short that there can be little doubt that their sterigmata were among the last to produce spores. The subhymenium is shown at *s*, and a waste spore at *w*.

The surface view of the exhausted hymenium shown at C corresponds to the section at A. The only elements we can clearly distinguish in it are the paraphyses *p*. The gelatinous remains of the basidia fill the spaces between the paraphyses and are

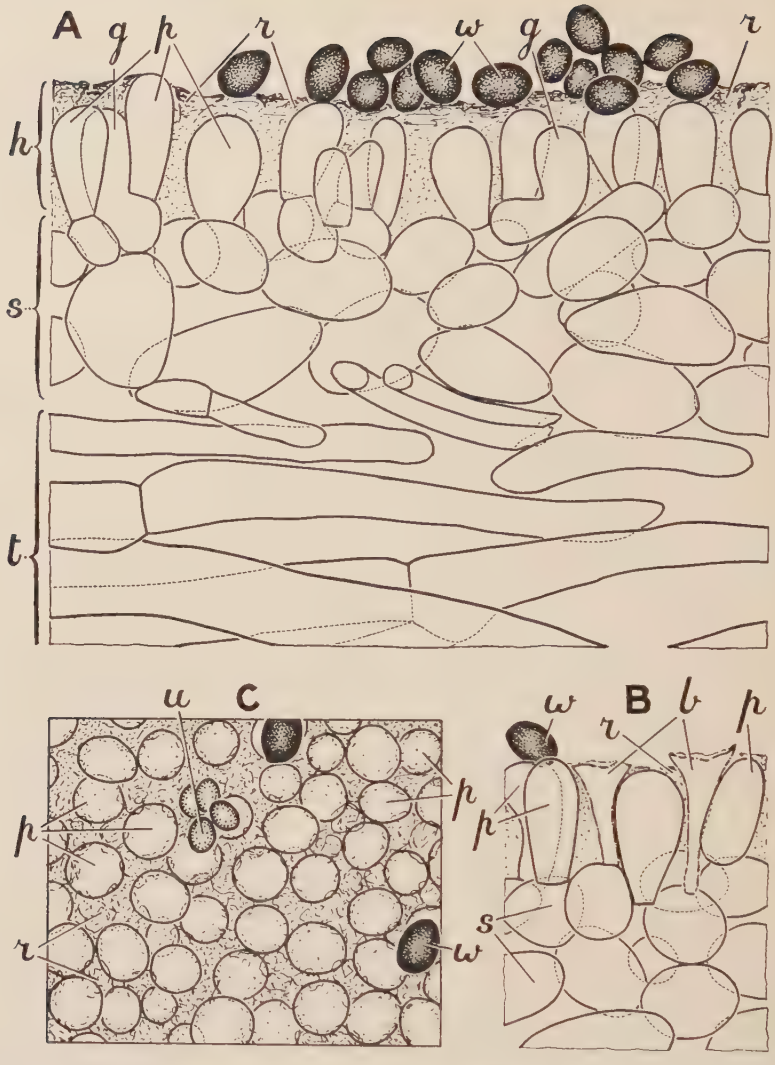

FIG. 152.—*Psalliota campestris* (wild form). To show the existence of paraphyses in a completely exhausted hymenium. The hymenium was examined a few hours after total exhaustion, before which the mushroom had shed spores for six days and six nights. A and B, transverse sections through the living hymenium ; C, a surface view of the same. Preparations mounted in water and drawn with aid of the *camera lucida*. In A, *h* is the hymenium composed of paraphyses, *p*, *g*, and of the gelatinised remains of basidia, *r*. The paraphyses *g g* appear to have been formed by mere extensions of two subhymenial cells. The waste spores *w* are lying on the hymenium. The subhymenium, composed of about three layers of swollen cells, is shown at *s*, and part of the trama at *t*. In B, the structure of the hymenium is similar to that in A except for the fact that the outlines of two short lately collapsed basidia could be definitely made out at *b*. The remains of other basidia are shown at *r*, paraphyses at *p*, a waste spore at *w*, and subhymenial cells at *s*. In the surface view C, the paraphyses are shown at *p*, and the gelatinised remains of the exhausted basidia at *r*. Lying on the hymenium are two fully pigmented and full-sized spores, *w*, and four unripe, unpigmented spores at *u*. Magnification 1,040.

indicated at *r*. A mature waste spore is present at *w*, and four very immature waste spores which failed to attain even full size are present at *u*. This surface view serves not only to demonstrate the presence of paraphyses, but also to show how numerous they are and how evenly distributed throughout the hymenium.

Secotium agaricoides.—In concluding this Chapter, I shall make mention of *Secotium agaricoides* (Czern.) Holl. (= *S. acuminatum* Mont.), a peculiar fleshy fungus which in some ways resembles a Puff-ball but which, from its mode of development as described by Conard, may be nothing more than a much modified Psalliota, possibly a near relative or direct descendant of the Common Mushroom.

Secotium agaricoides (Figs. 153, 154, 155) was first found in the Ukraine by Czerniaiev [1] in 1845. In 1882 it was found by Peck [2] in the United States of America and was described by him as *S. Warnei*. In 1903, Hollós,[3] in his *Gasteromycetes Hungariae*, treated of it at some length with the help of an excellent series of illustrations which showed its variability in form, size, and general appearance. This author examined some of Peck's specimens of *S. Warnei*, pronounced them to be identical with the European plants, and recorded *S. agaricoides* not only from Europe but also from Asia, Africa (Algeria), North America (Ohio to Wisconsin and Kansas), New Zealand, and Australia (Banks Peninsula). I can now add that the fungus has recently been found in Canada, by myself near Winnipeg (Fig. 155) and by Mr. Odell near Ottawa (Figs. 153 and 154).

The fruit-bodies of *Secotium agaricoides*, when found upon a grassy sward, look very much like small Puff-balls; for they are more or less spherical or oval, whitish, and closely adherent to the ground. However, they each possess what all true Puff-balls lack, namely, a stipe which continues upwards through the body of the sporophore as a columella. The body-wall (peridium) encloses a compact mass of branched and much folded lamellae instead of a capillitium (Fig. 154).

[1] B. M. Czerniaiev, "Nouveaux Cryptogames de l'Ukraine et quelques mots sur la flore de ce pays," *Bull. Soc. Imp. Nat. Moscou*, T. XVIII, 1845, pp. 132–157.

[2] C. H. Peck, "New Species of Fungi," *Bull. Torrey Bot. Club*, vol. ix, 1882, pp. 61–62.

[3] L. Hollós, *Gasteromycetes Hungariae*, Budapest, 1903; Leipzig, 1904, pp. 33–37, Plates III–VI *bis*.

At maturity the fruit-body, under dry climatic conditions (as at Winnipeg), may sometimes remain closed ; but usually it dehisces

FIG. 153. —*Secotium agaricoides*—a fungus resembling a Puff-ball, but closely allied to Psalliota. A, a fruit-body developing its spores. B, a normal fully-developed ripe fruit-body showing the peridium slightly separated from the stipe below and longitudinally cracked ; branched gills and spores, concealed under the peridium, now pulverulent. C, a fruit-body expanded to a much greater extent than is normal, its body thus resembling the expanded pileus of a Psalliota. Collected by W. S. Odell at Ottawa. Photographed by the Photographic Division of the Canadian Geological Survey. Natural size.

irregularly by means of one or more longitudinal rifts (Figs. 153, B, and 155) or by part, or occasionally the whole, of the base of the

peridium separating slightly from the stipe and columella after the manner of an agaric such as a Mushroom. The photographs reproduced in Figs. 153, B, and 155 show common types of mature fruit-bodies, while those reproduced in Figs. 153, C, and 154 show an amount of expansion beyond the ordinary.

After a median vertical section had been made through a fruit-

FIG. 154.—*Secotium agaricoides.* A vertical section through a ripe fruit-body which has expanded on the left side only. Exposed to view are: the peg-like stipe and its extension, the columella; the peridial flesh; and the pulverulent, spore-enclosing gills. Collected by W. S. Odell at Ottawa. Photographed by the Photographic Division of the Canadian Geological Survey. Natural size.

body freshly gathered at Winnipeg, the upper part of the columella turned brown on bruising and the anastomosing gill-plates greenish.

Conard [1] describes the general development of the fruit-bodies of *Secotium agaricoides* in the following words: "The youngest specimens are nearly globular, white, and smooth. Then comes a 'button stage,' with the upper portion slightly larger than the stalk and the surface still smooth. Later, the fertile portion increases greatly in height and diameter, leaving the free stalk as a mere basal projection. The superficial brown scales of the peridium appear only when near full maturity. The spores are fully mature

[1] H. S. Conard, "The Structure and Development of *Secotium agaricoides*," *Mycologia*, vol. vii, 1915, p. 95.

while the trama, peridium, and stalk are still fleshy. The old specimens, at least in our climate (Iowa), dry up and do not putrefy."

With the help of the microtome, Conard found that the development of a fruit-body of *Secotium agaricoides*, in its earliest stages, is precisely like that of *Psalliota campestris* and *P. arvensis* as described by Atkinson,[1] and not at all like that of Phallus and Mutinus. The hymenophore was distinctly seen as a horizontal ring of deeply-staining tissue within the globular fungus body of a sporophore only 3·5 mm. in diameter (Fig. 156, No. 1); and in another fungus-body, 9 mm. in diameter, the branched and anastomosing gills were found to run primarily in a radial direction and to be extending from the cap to the columella (Fig. 156, No. 2 [2]).

The spores are olive-green in the mass, ovoid, 7 μ long and 5 μ wide, smooth, thick-walled, and possessed of an apical germ-pore.[3] This pore is evidently homologous with the germ-pore that one finds in the thick-walled spores of Coprini, Panaeoli, Psalliotae, and other chromosporous Agaricineae. The basidia are tetrasterigmatic and quadrisporous, and a spore often carries with it a part of the sterigma as an appendage.[4]

"The mature gills," says Conard,[5] "are much branched and folded. The tramal tissue consists of long branching and nearly parallel hyphae, whose ultimate branchlets form the densely crowded basidia. There are no cystidia or other aberrant cells. From a fairly dense web in growing stages, the trama becomes looser toward maturity and finally becomes dry and fragile. From the above account it is clear that the carpophore of *Secotium agaricoides* presents in its origin and development an exact counterpart of that of Agaricus [6] (Atkinson, 1906, 1914). There is at first a universal veil like that of evolvate agarics (Agaricus, Armillaria, and Stropharia). There is an ill-differentiated partial veil. The origin of the hymenophore agrees precisely with that of all recently reported agarics except Hypholoma (Allen, 1906) and Coprinus

[1] G. F. Atkinson, "The Development of *Agaricus campestris*," *Bot. Gaz.*, vol. xlii, 1906, pp. 215–221; also, "The Development of *Agaricus arvensis* and *A. comtulus*," *Am. Journ. Bot.*, vol. i, 1914, pp. 3–22.

[2] H. S. Conard, *loc. cit.*, pp. 95–98.

[3, 4] *Ibid.*, p. 94.

[5] *Ibid.*, pp. 97–98.

[6] Agaricus = Psalliota.

(Levine, 1914). The marginal growth of the gill system is also familiar in the mushrooms. The columella comes into being exactly as does the stipe of mushrooms. Indeed, we might well speak of stipe and pileus of Secotium, rather than of peridium and columella. The basidia have the shape, size, and arrangement found in agarics. The copious branching of the gills exceeds anything seen in agarics. The failure of the cap and gills to expand, the drying up of the trama into a friable mass of tissues and spores, the olive-brown color of the spores, and the freedom of the spores to 'puff' when the exposed mass is touched, are all lycoperdinean characters."

FIG. 155.—*Secotium agaricoides*. A full-grown conico-cylindrical fruit-body showing its characteristically peg-like stipe and a longitudinal crack in the upper part of the peridium. Collected at Winnipeg by the author. Natural size.

A simple forking of the gills occurs in certain Agaricineae, *e.g. Russula furcata* and *Cantharellus cibarius*; but it is a perfectly normal phenomenon and in no way interferes with the liberation of the spores. On the other hand, an irregular branching and anastomosis of the gills sometimes occurs in *Pholiota erebia* (Fig. 157), etc., and I myself have observed it in a *Psalliota campestris* fruit-body which I gathered in a field near Banbury, England, and in some large *Coprinus niveus* fruit-bodies which I grew in pure cultures on horse dung at Winnipeg. Here the lamellar irregularities were certainly abnormal and seriously interfered with spore-liberation. I am inclined to believe that the copious branching and anastomosis of the gills in *Secotium agaricoides* arose in the first place as an abnormality affecting simple radial gills and that it is therefore comparable with the

abnormalities in *Pholiota erebia*, *Psalliota campestris*, and *Coprinus niveus* just described.

"On the whole," concludes Conard,[1] "*Secotium agaricoides* would best be placed near to Agaricus (Psalliota), either in the Agariceae or Marasmieae of Hennings (1897). It clearly falls within the Agaricaceae of Maire (1902). It is to be regarded as a primitive

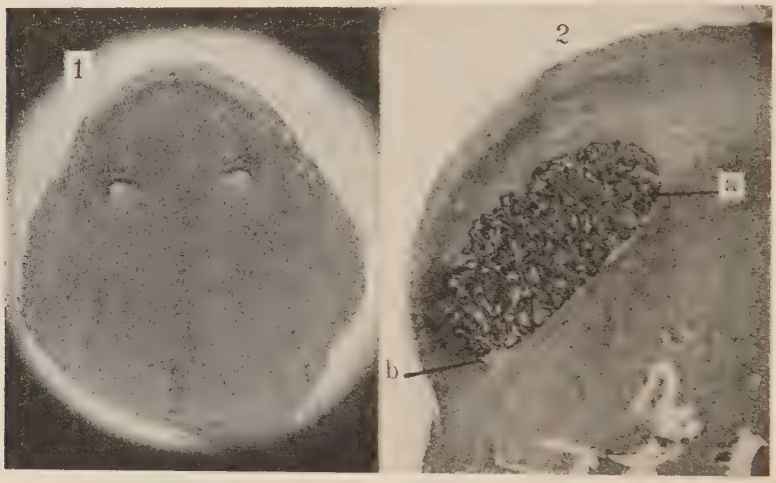

FIG. 156.—*Secotium agaricoides*. Stages in the development of two fruit-bodies. No. 1, a median longitudinal section of a fruit-body 3·5 mm. in diameter, showing the fundament of the hymenophore and the gill-chamber. No. 2, the left half of a median longitudinal section of a fruit-body 9 mm. in diameter, showing a ring of well-formed gills extending from the cap toward the columella. The gills are much branched and anastomosing, and they run primarily in a radial direction. At *a* they are attached to the columella and are therefore decurrent; and at *b* they are extending centrifugally. Photographed by S. Conard.

or arrested agaric—perhaps a paedogenic form, reaching its reproductive maturity in the 'button' stage."

It seems, therefore, as a result of Conard's investigation, that we are justified in thinking of *Secotium agaricoides* as a fungus which superficially resembles a Puff-ball (Lycoperdon), but which, nevertheless, has been derived from an ancestor which must have had a structure practically identical with that of the Common Mushroom and its allies. This ancestor, doubtless, possessed a simple radial gill-system, expanded its pileus in the usual way, and

[1] H. S. Conard, *loc. cit.*, p. 101.

shot its spores from its basidia into the interlamellar spaces, the production and liberation of the spores thus continuing for a spore-fall period occupying several days. In this ancestor, in the course of evolution, we must suppose that a series of changes took place which profoundly altered the mode of spore-liberation and rendered the beautiful gunnery of the basidia superfluous and useless. Owing, possibly, to one or more mutations: (1) the gills became branched and anastomosing; (2) the pileus ceased to expand in the usual way at maturity; (3) the spores ceased to be shot away from their basidia and, on ripening, merely accumulated in the gill-folds and cavities; (4) the pileus-flesh became tougher and more resistant to decay; and (5) the liberation of the spores imprisoned in the gill-folds and cavities came to be effected by the gills drying and becoming friable and by the dry spore-powder falling through cracks in the unexpanded pileus. Thus, to a certain extent, the fungus came to resemble a Puff-ball in both its outward form and its mode of evacuating its spores. However, whilst a Puff-ball, *e.g. Lycoperdon gemmatum* or *L. giganteum*, gives one the impression of having a structure which is beautifully adapted to secure the liberation of the spores,[1] one does not gain a similar impression on beholding the irregularly cracking, often misshapen fruit-bodies of *Secotium agaricoides*. These fruit-bodies rather look like monstrosities, indeed, as if they had recently changed their mode of spore-liberation but were still structurally imperfectly adapted to the new functional demands made upon them.

FIG. 157.—*Pholiota erebia*. An abnormal fruit-body: the gills, instead of being simple, exhibit irregular branching and anastomosis. Photographed at Scarborough, England, by A. E. Peck. Natural size.

[1] *Cf.* these *Researches*, vol. i, 1909, p. 258.

GENERAL SUMMARY

THE FOLLOWING IS A SUMMARY OF THE MORE IMPORTANT RESULTS OBTAINED DURING THE INVESTIGATIONS

Chapter I.—Typically, the hymenium of Hymenomycetes consists of basidia, paraphyses, and cystidia. Two nuclei fuse together in each young basidium, and every basidium eventually produces spores. There is no nuclear fusion in paraphyses and cystidia, and these elements are sterile from the first.

In all Hymenomycetes, the spore has a little projection or *hilum* at its base, which projects toward the axis of the basidium. From this hilum, a few seconds before spore-discharge, a tiny fluid drop is excreted. The drop grows to a maximum size which is usually equal to about one-half the diameter of the spore. Then the spore is shot violently away from its sterigma. The drop clings to the spore and is always carried away by it. Sometimes the drop is not excreted at all and sometimes the excretion is excessive. Under these conditions the spores are never discharged from their sterigmata.

The author discusses, but is not able to explain satisfactorily, the mechanism of spore-discharge. The fluid drop excreted by the hilum of the spore is not improbably an indication of some chemical or physical change taking place in the cell-wall.

A basidium never produces more than one generation of spores upon its sterigmata. Direct observations made upon living disterigmatic and tetrasterigmatic basidia (Psalliota, Calocera, Panaeolus, etc.) show that a basidium, 15–30 minutes after discharging the last spore it bears, collapses and dies.

There is a relation between the volume of a basidium and the total volume of the spores which it bears. In *Psalliota campestris* (cultivated form) the volume of a spore of a monosterigmatic basidium is twice that of one of the spores of a disterigmatic basidium.

In the Hymenomycetes, the sterigma, in association with the hilum of the spore, is to be regarded as an organ specialised for bringing about violent spore-discharge. In the Gastromycetes, in which the spores are not violently discharged, the sterigmata are either suppressed or imperfectly developed, and the spore-hilum is altogether lacking. Typically, in the Hymenomycetes, each basidium bears four spores separated from

one another by well-marked spaces ; whereas, in the Gastromycetes, each basidium often bears more than four spores, and the spores are often crowded together on the end of the basidium-body so that at maturity they touch one another. This difference, again, is correlated with the fact that in the Hymenomycetes the spores are violently discharged, whereas in the Gastromycetes they are not.

A toy balloon resembles a spore in having an enormous surface area relatively to its mass. The author has invented a *balloon gun* with toy balloons for projectiles. The trajectory of a balloon shot horizontally resembles the trajectory (sporabola) of a spore shot horizontally from its sterigma.

The rates of fall of thistle-down, basidiospores, and bacteria have been compared. The spores of Hymenomycetes fall much more slowly than thistle-down, but much faster than bacteria. To fall a single inch in still air certain very small bacteria require somewhat more than three hours. To calculate the rate of fall of bacteria the author has employed the equation for Stokes' Law as corrected by Millikan.

Chapter II.—The interval of time which elapses between the first appearance of a spore on the end of its sterigma as a tiny rudiment and the moment of spore-discharge has been measured for a number of Agaricineae. In *Collybia velutipes* it was found to be only about 47 minutes and in *Panaeolus campanulatus* about 7 hours and 30 minutes. The interval is usually very short (50–90 minutes) for spores having thin, smooth, colourless walls and much longer (3–9 hours) for spores having thick, pigmented walls or walls which are polyhedral or warted. In general, the interval is short for the spores of the Leucosporae and long for the Chromosporae (chromosporous Agaricineae). The longest interval observed was about 32 hours for *Coprinus sterquilinus*. In this fungus, on any small area of the hymenium, the basidia all develop their spores simultaneously.

The ripening of a spore, after the spore has attained full size, takes a longer time than the growth of the spore to full size. Thus in *Collybia velutipes* the spores take about 15 minutes to grow to full size and a further 32 minutes to ripen and become discharged ; and in *Psalliota campestris* the spores take 40 minutes to grow to full size and a further period of about 7 hours and 20 minutes to ripen and become discharged.

Chapter III.—When the parasite *Hypomyces lactifluorum* attacks *Lactarius piperatus*, the host fruit-bodies grow to normal size but fail to develop gills and remain completely sterile. On the other hand, the Hypomyces gives rise to great numbers of perithecia on the under side of the pileus. The author discusses the relations between the parasite and its host, and describes his observations upon the discharge of spores from the perithecia.

Occasionally the fruit-bodies of certain Hymenomycetes grow to full size but remain partially or completely sterile. Some fruit-bodies of

Coprinus lagopus which developed no spores at all were found to possess basidium-bodies but neither sterigmata nor spore-rudiments. The author discusses the possible cause of sterility.

It is suggested that the monstrous fruit-bodies of *Polyporus rufescens* owe their abnormal form to a loss of power to respond to geotropic stimuli.

The pileus of a *Coprinus sterquilinus* fruit-body was successfully grafted upon the decapitated stipe of another fruit-body of the same species ; but attempts to graft the pileus of one species of Coprinus upon the stipe of another species failed.

Coprinus lagopus, which under favourable conditions produces large fruit-bodies, 100–200 mm. high, under less favourable conditions produces dwarf fruit-bodies which may have stipes only 1–10 mm. high and expanded pilei only 0·75–3 mm. in diameter. These minute fruit-bodies, which may lack cystidia, develop and liberate a small number of perfect spores which, if sown on favourable nutrient media, give rise to large normal fruit-bodies one hundred or more times larger than the dwarfs. The dwarf fruit-bodies of *C. lagopus* have been regarded by certain systematists as belonging to an independent species.

At Winnipeg *Marasmius oreades* has been successfully cultivated for food purposes from spawn on a soil-covered bed of manure. The author describes how the bed was made and the large abnormal fruit-bodies which appeared upon it.

Chapter IV.—The spore-fall period for *Coprinus curtus*, which has small fruit-bodies (expanded pilei 2·5–15 mm. wide) occurring on horse dung, is extremely brief, being only from 30 minutes to 2 hours and 30 minutes in length. The fruit-bodies are produced in diurnal crops, and the spores are usually liberated about the middle of the morning.

The escape of the white spore-clouds from the pilei of *Armillaria mellea* was successfully observed by the author with the naked eye, under natural conditions in a wood.

From the fruit-bodies of *Hydnum septentrionale* there is probably not " a simultaneous liberation of spores followed by a period of rest," as has been supposed ; but, on the contrary, the spores are probably liberated in a constant stream, as in the Agaricineae, the Polyporeae, and Hymenomycetes in general.

The fruit-body of *Fomes fomentarius* develops a new annual tube-layer in the autumn, but the production and liberation of spores from it is delayed until spring. This discovery, originally made by J. H. Faull, has been confirmed by the author. Faull has also discovered that, in *F. fomentarius*, each annual tube-layer may produce a crop of spores for four years in succession. The form and mode of growth of a *F. fomentarius* fruit-body is profoundly modified by various reactions to the stimulus of gravity. The attachment of a *F. fomentarius* fruit-body to the mycelium in the trunk of a tree is localised at the back

of the pileus-flesh at the upper end of the fruit-body, and the attachment of the rest of the fruit-body to the tree-trunk is merely by adhesion to the bark.

Fomes igniarius develops a new layer of hymenial tubes each summer and has a summer spore-discharge period of somewhat more than two months' duration.

In Manitoba, owing to winter frost, the spore-discharge period of *Daedalea confragosa* and certain other lignicolous Hymenomycetes is often divided into two parts, one autumnal and the other vernal.

In the Polyporeae, the pilei : (1) may be solitary as in *Fomes officinalis*, (2) may be imbricated as in *Polyporus sulphureus*, or (3) may form part of a compound fruit-body as in *P. umbellatus*. The author discusses the significance of these arrangements.

Chapter V.—*Fomes applanatus* is an important wood-destroying fungus which attacks upwards of fifty species of trees. The author treats of its biology, more especially of its production and liberation of spores, in the light of the investigations made by J. H. White and by himself. The basidiospore should not be regarded as a chlamydospore. *Fomes applanatus* may produce 10 successive annual tube-layers ; *F. officinalis*, 45 ; and *F. igniarius*, 80.

Owing to the narrowness, length, and crowding of the hymenial tubes a fruit-body of *Fomes applanatus* has a very large hymenial surface. White found that a large fruit-body liberated about 30,000,000,000 spores in 24 hours and that the spore-fall period had a duration of six months (the longest known). The visible emission of spore-clouds from the pileus has been observed by White at Ottawa and by the author at Kew. The length of the spore-fall period in the Hymenomycetes is roughly correlated with the mechanical consistence of the fruit-bodies, the most watery fruit-bodies having the shortest spore-fall period, and the most woody the longest. The number of spores liberated per annum by a very large fruit-body of *Fomes applanatus* is of the same order of magnitude as the number liberated from a fruit-body of the Giant Puff-ball. The great length of the spore-fall period appears to be correlated with the long-continued growth in length of the hymenial tubes ; but a full explanation of the duration of the spore-fall period can be given only after the organisation of the hymenium has been elucidated in detail.

The production of vast numbers of spores by the fruit-bodies of wood-destroying fungi appears to be necessary to permit of these fungi overcoming the difficulties of invading new woody substrata with sufficient frequency to maintain themselves under natural conditions.

Chapter VI.—In the Hydneae, the Tremellineae, and the Clavarieae, the form of the fruit-body is intimately correlated with the size and strength of the basidial guns which discharge the spores. In the Exobasidieae, the absence of a fruit-body is correlated with the

fact that the fungi in this group are parasitic on shrubs and produce their hymenial layers high above the ground on the surface of living leaves, etc.

In the Hydneae, the increase in the surface-area of the hymenium beneath the pileus has been effected by the development of positively geotropic spinous processes (teeth), instead of by gills as in the Agaricineae, or by hymenial tubes as in the Polyporeae. Each spore is discharged from its sterigma only after the emission of a drop of fluid from the hilum, as in other Hymenomycetes.

The gelatinous consistence of the fruit-bodies of the Tremellineae is correlated with the lignicolous habit of the group. When sticks bearing Tremellineae dry up, the fruit-bodies dry up too but retain their vitality. When rain comes again, the water is rapidly absorbed, not by *capillarity* as in Lenzites and other non-gelatinous lignicolous fruit-bodies, but by *imbibition*. After absorbing water and expanding, a gelatinous fruit-body immediately resumes its work of producing and liberating spores.

The period between the first appearance of a spore on its sterigma as a tiny rudiment and its discharge with drop-excretion is very short in the Tremellineae: 1 hour 20 minutes in *Calocera cornea*; 1 hour 15 minutes in *Exidia albida* and 50 minutes in *Dacryomyces deliquescens*. This rapidity of spore-development is correlated with the fact that the spore-walls are thin and smooth, and with the fact that the fungi are lignicolous.

The author discusses the problem of septation in the basidia of the Tremellineae and attempts to solve it from the physiological point of view.

The spores of the Tremellineae are more violently discharged than those of the non-tremelloid Hymenomycetes, but somewhat less violently than those of the Uredineae. In violence of spore-discharge the Tremellineae thus take up an intermediate position between the Hymenomycetes in general and the Uredineae. In those Tremellineae in which the hymenial surface often looks more or less upwards, great violence of spore-discharge is distinctly advantageous from the point of view of the dissemination of the spores by the wind.

The author redescribes the basidial and oidial fruit-bodies of *Dacryomyces deliquescens* and points out that, hitherto, they have been regarded by certain systematists as belonging to different species.

In the Clavarieae, the hymenium is exposed on the surface of the fruit-bodies. Some simple fruit-bodies, *e.g.* those of *Clavaria pistillaris*, are obconic in form, so that the hymenium looks more or less downwards. In compound Clavariae the successive branches are usually more or less obconic in form, so that here again the hymenium tends to be so placed that it looks horizontally more or less downwards, thus favouring the dispersal of the spores. In most Clavariae the basal

parts of the fruit-bodies, the tops or tips of the ultimate branches, and the upper surfaces in the angles of each fork are usually sterile. In the Clavariae the discharge of the spores from the basidia is accompanied by a drop excretion from the spore-hilum, as in other Hymenomycetes.

Sparassis has its hymenium restricted to the lower surfaces of its laminae. In this it resembles Stereum, but it may have been evolved from a Clavaria.

Calocera resembles Clavaria in its form and in the small distance to which its spores are shot from their sterigmata, but it differs from Clavaria in being subgelatinous, in becoming horny on drying, in reviving after desiccation, and in possessing long cylindrical bifurcated basidia.

The galls formed by Exobasidium species upon their hosts are advantageous to the parasites in extending the surfaces over which they may spread their hymenium.

Chapter VII.—The Red Squirrel of North America not only feeds on the seeds of fir-cones, hazel-nuts, etc., but is also an habitual mycophagist. In the late autumn, it often collects fleshy fungi in large numbers for its winter supply of food, and it stores these fungi sometimes *en masse* in holes in tree-trunks, old birds' nests, etc., and sometimes on the branches of certain trees. The fruit-bodies hung out in the branches of trees dry up and are thus preserved; and squirrels have been watched eating them during the winter.

Chapter VIII.—Slugs attack and feed upon most species of fleshy Hymenomycetes occurring in woods, including *Amanita muscaria* and *A. phalloides* which are poisonous to human beings, and *Pluteus cervinus* the gills of which are provided with numerous cuspidate cystidia. The attacks of slugs often interfere seriously with, and sometimes entirely prevent, the production and liberation of spores by individual fruit-bodies. Most species of fleshy fungi are in no way protected against slugs. Very many species of fleshy fungi do not depend on slugs for the dissemination or germination of their spores.

Slugs find the fungi upon which they feed by their sense of smell. Chemotactic experiments made upon *Limax maximus* with *Phallus impudicus*, *Boletus scaber*, *Russula nigricans*, etc., in which the fruit-bodies were set out on bare gravel, showed that this slug can find various fruit-bodies at night by its sense of smell even when the fruit-bodies are 20 feet distant.

Chapter IX.—In the Agaricineae there are two main types of organisation for the production and liberation of spores: (1) the *Aequi-hymeniiferae* or Non-Coprinus Type, and (2) the *Inaequi-hymeniiferae* or Coprinus Type; and each Type includes several distinct Sub-types.

In the Aequi-hymeniiferae: (1) usually the gills are relatively thick; (2) the gills are wedge-shaped in cross-section; (3) the gills are positively geotropic; (4) the hymenium looks downwards to the earth; (5) every

part of the hymenium produces and liberates spores during the whole period of spore-discharge; and (6) the gills are not destroyed from below upwards by autodigestion. The name *Aequi-hymeniiferae* refers to the *equal* development of the different parts of the hymenium.

In the Inaequi-hymeniiferae: (1) the gills are very thin; (2) the gills are not wedge-shaped but, on the whole, parallel-sided or sub-parallel-sided; (3) the gills are not positively geotropic; (4) usually the hymenium on one side of a gill at maturity looks slightly downwards and that on the other side slightly upwards; (5) the spores ripen in succession from below upwards on each gill; (6) the spores are discharged in succession from below upwards on each gill; and (7) autodigestion proceeds from below upwards on each gill and removes those parts of the gills which have become spore-free and which, if they continued in existence, would become mechanical hindrances to the fall of the remaining spores. The name *Inaequi-hymeniiferae* refers to the *unequal* development of the different parts of the hymenium, the production and liberation of the spores proceeding in a zone-wise manner from below upwards on each gill.

Chapter X.—In the Panaeolus Sub-type the gills are *mottled*. Mottling is an expression of the fact that the hymenium is made up of a mosaic-work of small irregular local areas, the basidia in the darker areas bearing older pigmented spores and those in the lighter areas either no spores at all or spores which are younger and as yet unpigmented. With the discharge of the spores, a dark area turns light; and, with the ripening of the spores, a light area turns dark.

Mottling of the gills occurs not only in Panaeolus but also in Anellaria, Psilocybe, Hypholoma, Stropharia, Psalliota, Cortinarius, Crepidotus, Flammula, and Pholiota.

The changes taking place in one and the same piece of hymenium of a living gill of *Panaeolus campanulatus* were observed during three days and three nights with a horizontal microscope. It was discovered that each area of the hymenium gives rise to a series of successive generations of spore-bearing basidia, each area changing from black to white alternately many times in succession.

The fall of spores from a fruit-body of *Panaeolus campanulatus* continues for about 8–11 days; and it is the development of successive generations of basidia on the local hymenial areas which enables spores to be discharged as an uninterrupted spore-stream during the whole of the spore-discharge period.

In any small area of the active hymenium of *Panaeolus campanulatus* (0·2 square mm.), the hymenial elements can all be placed in one or other of the following five classes: (1) past-generations basidia, (2) present-generation basidia, (3) coming-generation basidia, (4) future-generations basidia, and (5) paraphyses. This analysis greatly simplifies our conception of the organisation of the hymenium of *Panaeolus*

campanulatus and applies equally to all other members of the Panaeolus Sub-type.

The author has studied the hymenium of *Panaeolus campanulatus*: (1) before the development of the spores, (2) in the middle of the spore-fall period, and (3) at the end of the spore-fall period when the hymenium has become exhausted; and he has illustrated his analyses with a complete series of drawings, showing the hymenium both in surface view and in cross-section and indicating the time and space relations of all the elements.

The paraphyses of *Panaeolus campanulatus*, unlike the young basidia, are destined from the first to remain sterile. They are about equal in number to the basidia; but they differ from the basidia in: (1) size, (2) position, (3) form (as they grow older), (4) early vacuolisation and ultimate disappearance of their cytoplasm except for a very thin wall-layer, (5) never developing either sterigmata or spores, and, doubtless, also, (6) in the non-fusion of the two nuclei with which they are at first provided. As, during the spore-fall period, more and more basidia discharge their spores and collapse, the paraphyses swell up and to a large extent fill up the gaps made in the hymenial layer by the shrinkage of the exhausted basidia. In general, the paraphyses appear to act as mechanical supports and nurse-cells for the spore-bearing elements.

A basidium, about 20 minutes after discharging the last of its four spores, collapses: its convex end bearing the sterigmata sinks down and becomes concave, thus drawing the sterigmata into a concavity. The shaft of the basidium then shrinks laterally and the four sterigmata become melted down to sterigmatic stumps. Exhausted basidia can be recognised in cross-sections by the flat rims of their concave ends and by their shrunken shafts, and in surface view by their lack of contents and by their sterigmatic stumps.

Irregular waves of hymenial development pass across the mottled surface of each gill. These waves are comparable with the undulations which may be observed in the epithelium which produces spermatozoa in the testicular tubules of the Mammalia.

The wasted spores, *i.e.* those which are not properly discharged from the sterigmata and which cling to the hymenium, form but a very small percentage of the total number of spores produced.

The author shows that the protuberancy of the mature basidia, the collapse of the exhausted basidia, the relative positions of spores on individual basidia with 2–8 sterigmata, and the relative positions of the spore-bearing basidia of a single generation are all factors making for the success of the fruit-body as an organ for the production and liberation of the spores.

Many Hymenomycetes are known in which the basidia are disterigmatic and bisporous; but *Coprinus narcoticus* is at present the

only known hymenomycetous species in which the basidia are regularly tristerigmatic and trisporous.

Panaeolus campanulatus lacks pleurocystidia, but possesses a fringe of cheilocystidia along the free edge of each gill. The cheilocystidia excrete mucilaginous globules.

Chapter XI.—*Stropharia semiglobata* belongs to the Panaeolus Sub-type, and its organisation for the production and liberation of spores very closely resembles that of *Panaeolus campanulatus*. The author describes the hymenium in detail and illustrates it with drawings showing surface-views and cross-sections. The hymenial elements all belong to one of six classes: (1) past-generations basidia, (2) present-generation basidia, (3) coming-generation basidia, (4) future-generations basidia, (5) paraphyses, and (6) cystidia. The efficiency of a given area of the hymenium was determined by observing the total number of spores which the area produced and the percentage of the spores which failed to be properly discharged.

Chapter XII.—*Anellaria separata* belongs to the Panaeolus Sub-type, and its organisation for the production and liberation of spores resembles that of *Panaeolus campanulatus* and *Stropharia semiglobata*. The author describes the fungus and, among other illustrations, shows a photomicrograph of the spores belonging to the present spore-bearing generation of basidia situated in one of the dark areas of the mottled hymenium. This is the first photograph of the kind ever published.

Chapter XIII.—The author gives a full description of the general characters of the *Psalliota campestris* fruit-body, including the mottling of the gills, and points out that the gills are not truly deliquescent during the spore-fall period. Dead fruit-bodies, enclosed in crystallising dishes, give off ammonia gas during putrefaction.

The occurrence of *Psalliota campestris* in *fairy rings* affords evidence that new substrata below the turf are not easily invaded by mycelium produced from spores.

The author discusses the principles involved in the construction of the stipe and of the pileus-flesh in relation to their function, the radial arrangement of the gills, the depth and thickness of the gills, the presence of the gill-chamber, the conditions of origin of the fruit-bodies, the fate of fruit-body rudiments, and the effect of dry weather on fruit-body development.

Psalliota campestris possesses finely mottled gills and belongs to the Panaeolus Sub-type. The organisation of its hymenium for the production and liberation of spores closely resembles that of *Panaeolus campanulatus* and *Stropharia semiglobata*. For the first time, the author describes the structure of the hymenium in detail and illustrates it with drawings showing both cross-sections and surface-views. For the study of the hymenium, *Psalliota campestris* affords much less favourable material than *Panaeolus campanulatus* or *Stropharia semiglobata*,

owing to the relative smallness of its basidia and paraphyses and the consequent denser packing of these elements.

The spore-discharge period of a wild *Psalliota campestris* was observed to be of 4–6 days' duration. Spores begin to be discharged from a fruit-body when the gills are pink and the pileus is still expanding, and they continue to be discharged even when the top of the pileus has become quite flat and the gills have turned dark chocolate-brown. The number of spores produced by a large Mushroom was calculated to be upwards of 10,000,000,000.

In *Psalliota campestris*, just as in *Panaeolus campanulatus*, irregular waves of hymenial development constantly pass over the surface of each gill, thus changing the pattern of the mottling; and the elements of the hymenium can all be referred to one or other of the following five classes: (1) past-generations basidia, (2) present-generation basidia, (3) coming-generation basidia, (4) future-generations basidia, and (5) paraphyses.

In *Psalliota campestris*, as in *Panaeolus campanulatus*, the paraphyses are destined to be sterile from the first. They become vacuolated early and swell up considerably during the gradual exhaustion and collapse of the basidia. At the end of the spore-discharge period, all the basidia are collapsed and dead, but all the paraphyses are living.

The basidia of wild forms of *Psalliota campestris* are usually tetrasterigmatic and quadrisporous, whilst the basidia of cultivated forms are usually disterigmatic and bisporous.

In the hymenium of cultivated forms of *Psalliota campestris* a certain proportion of the basidia are usually monosterigmatic and unisporous. The unisporous basidia are equal in size to the bisporous: but the spore of a unisporous basidium has about twice the volume of one of the spores of a bisporous basidium. A cultivated Mushroom therefore has spores of two sizes, large and small.

The development of the four spores on a basidium of a wild Mushroom, from their first appearance as tiny rudiments to their discharge, was observed to occupy about 7·5 hours. A single spore (1) takes 30–40 minutes to grow from a tiny rudiment to full size, (2) remains colourless for the next two hours, (3) gradually becomes pigmented during the next two hours, (4) remains in the fully pigmented condition on the end of its sterigma for a further 3 hours and about 10 minutes, and (5) is then discharged. The discharge of a Mushroom spore takes place with drop-excretion as in other Hymenomycetes.

In *Psalliota campestris* there is no plane sharply dividing the subhymenium from the hymenium; but the subhymenium passes gradually into the hymenium, owing to the fact that the basidia are attached to subhymenial cells at different depths.

Secotium agaricoides resembles a Puff-ball in general appearance, but is nevertheless closely allied to Psalliota.

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